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MALACOLOGICAL REVIEW

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- Vol. 4: Conidae (cone shells)
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- Suppl. 1: Freshwater gastropods of Taiwan
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THE EMBRYONIC SHELL SURFACE SCULPTURE OF *GOCEA* AND *VALVATA*¹

S. Hadžišće, C. M. Patterson, J. B. Burch and P. T. LoVerde

ABSTRACT

The surface sculpture of the embryonic shell of *Gocea ohridana* and 4 species of *Valvata* (*V. hirsutecostata* and *V. relictata* from Lake Ohrid, Yugoslavia, and *V. tricarinata perconfusa* and *V. humeralis* from North America, the latter being Pleistocene fossil specimens) are described and compared. The embryonic shell sculpture of *Gocea* consists of many closely spaced small pits, while in the 4 *Valvata* species it is made up of prominent parallel spiral striae. This embryonic pattern in the Valvatidae seems to be a constant and conservative character. Because of the basic difference in the embryonic whorls of *G. ohridana*, it seems unlikely that *Gocea* is a member of the Valvatidae, where it has recently been assigned. The apical microsculpture of *Gocea* is very similar to that reported previously for 3 marine mesogastropods in the superfamilies Cerithacea and Cypraeacea. The significance of this similarity is not presently known. ADDENDUM: After this paper was in page proof, observations were made on the Lake Ohrid hydrobiid *Ohridohoratia pygmaea* and on 2 additional species and a subspecies of *Valvata* (*V. baicalensis*, *V. sincera sincera* and *V. s. ontariensis*). These additional observations augment our previous observations and conclusions.

Gocea ohridana Hadžišće is a tiny operculated prosobranch gastropod from the "sublacustrine interlithal" zone of ancient Lake Ohrid in Yugoslavia. It has a peculiar shell which is partially uncoiled, i.e., the whorls after the first are not peripherally attached. In this respect it resembles some specimens of several members of the mesogastropod family Valvatidae, e.g., *Valvata sincera ontariensis* Baker of Canada and *V. baicalensis* Gerstfeld of Lake Baikal, Siberia.

In the original description of the new genus and new species, *Gocea ohridana*, Hadžišće (1956a) placed it in the rissoacean family Hydrobiidae, principally because of its radular characteristics. Hadžišće (1956b) later placed *Gocea* in the subfamily Hydrobiinae as well. Stanković (1960: 190) suggested that *Gocea* "... is in reality a *Horatia* [a member of the hydrobiid subfamily Hydrobiinae according to Radoman (1955)] judging by the organization of the radula." Taylor (1966) placed *Gocea* in his new hydrobiid subfamily Cochliopinae and new tribe Horatiini. However, Radoman (1962, 1969) disagreed with the placement of *Gocea* in the Hydrobiidae, contending that instead it belongs to the Valvatidae. In his 1962 paper (p 91) he said [our translation to English from Serbo-Croatian], "Anatomical as well as conchological data show that *Gocea ohridana* Hadžišće 1956 does not belong to the family Hydrobiidae as determined by Hadžišće 1956, but it belongs to the family Valvatidae. The question remains open as to whether this species belongs to the genus *Valvata* or to a separate genus." In 1969, Radoman repeated this opinion, stressing that it is another example of incorrectly determining systematic status on conchological characters. An der Lan's (1971) suggestion that *Gocea* was derived

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from Miocene *Gyraulus* deserves no consideration (except that the so-called *Gyraulus* to which he refers are probably hydrobiids, and as hydrobiids are possibly related to *Gocea*).

Since for various reasons we do not agree with Radoman's taxonomic placement of *Gocea*, we have decided to compare other characters. One easily studied conchological aspect is that of the natural surface markings or sculpture of the embryonic shell (e.g., see Solem, 1970; Fretter & Pilkington, 1971; Robertson, 1971; Gittenberger, 1972), characteristics which have been considered constant and conservative in the freshwater ancyliids (Burch & LoVerde, 1974; Burch, 1974, 1975). In this regard, the apical whorls of *Valvata* previously have been described from observations with the light microscope as being spirally striate (e.g., see Baker, 1928; Binder, 1966, 1967). If *Gocea* is a valvatid, then one would assume that it also has a spirally striate embryonic shell. This paper presents our observations using a scanning electron microscope (SEM) on the embryonic whorls of shells of *G. ohridana* and 4 species of *Valvata*.

MATERIALS AND METHODS

The specimens of *Gocea ohridana* studied with the scanning electron microscope (SEM) were from Lake Ohrid at St. Naum in the sublacustrine interlithon.

For comparison with *Gocea*, the following species of *Valvata* were studied.

Valvata hirsutecostata Polinski. From Lake Ohrid, Macedonia (Yugoslavia), collected at Kalishta in May, 1973.

*Valvata relict*a (Polinski). From Lake Ohrid, Yugoslavia, collected at Kalishta in May, 1973.

Valvata tricarinata perconfusa Walker. UMMZ 99230. From Two-mile Pond, Niagara, Ontario, Canada, collected by A. C. Billups.

Valvata humeralis (Say). UMMZ 229974. Pleistocene fossils collected by R. C. Bright in 1958 at T11S, R41E, Section 30, Bannock County, Idaho (U.S. Geological Survey Cenozoic locality 22408).

The shells selected for this study were as young as possible, so that their sculpture would be less affected by abrasion and erosion. The shells were cleaned by immersing them in sodium hypochlorite (commercial "Clorox"), brushing the nuclear whorls with a fine brush and then passing them through several rinses of distilled water. After cleaning, the shells were dried and affixed with aluminum paint to the holder to be used in the SEM. The shells were coated with gold in a vacuum evaporator by ionizing radiation and viewed and photographed with a JEOL (Ltd.) JSM-U3 scanning electron microscope. Photographs were taken at X300, X600, X1000 and X1200 with Polaroid P-51 P N film.

OBSERVATIONS

The surface sculpture patterns of the nuclear whorls of *Gocea ohridana* and the 4 species of *Valvata* are given below.

Gocea ohridana (Fig. 1). The embryonic shell consists of 1 1/2 whorls and ends abruptly (Fig. 2), the neanic whorl continuing from its termination. The nuclear 1 1/2 whorls are densely and uniformly pockmarked with shallow pits, the density of the pits being about 100-120 per 0.1 mm². The pits are polygonal in outline (most often pentagonal), and mostly vary between about 0.005 and 0.007 mm in diameter. Over most of the surface these pits are rather flat-bottomed, but near



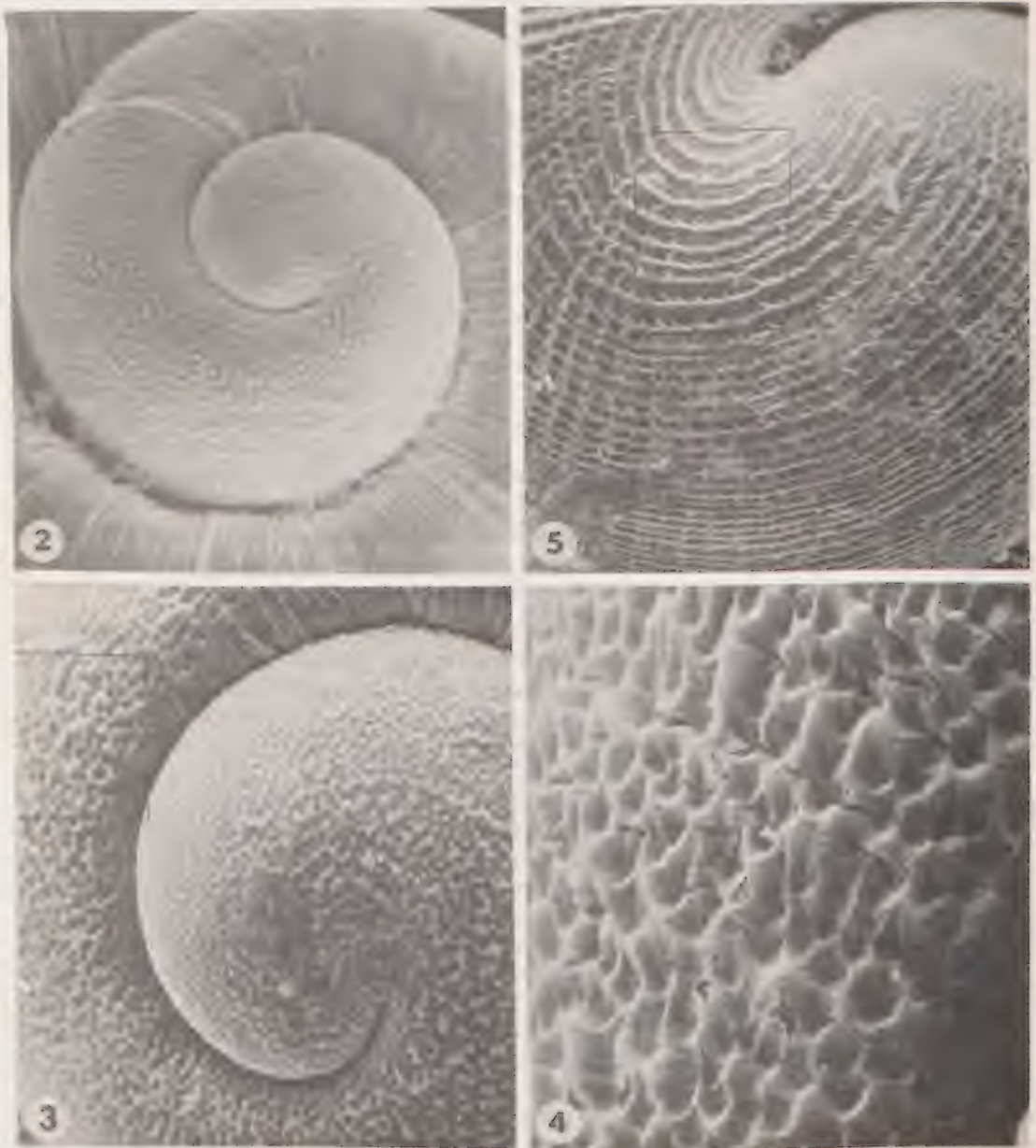
FIG. 1. Three views of the shell (with operculum) of *Gocea ohridana*. Scale line = 1 mm.

the distal end of the embryonic whorl they become deeper and are more conical inside (Fig. 4). In this area, close to the beginning of the neanic whorls, a few short, relatively deep, transverse grooves occur. The pits go right to the distal terminus of the embryonic shell, but they do not continue beyond it. The surface sculpture of the adjoining neanic whorl stands in striking contrast to that of the embryonic shell. The external surface of the neanic shell totally lacks pits, but instead is covered with low transverse growth lines or wrinkles, over which can be observed faint, somewhat irregular spiral indentations.

Valvata hirsutecostata. The termination of the embryonic shell and the beginning of the neanic shell in this species is not so clearly distinct as in *Gocea ohridana*. However, if we assume that the diminution of spiral sculpture marks the beginning of the neanic whorls, the embryonic shell appears to have a little more than 1 whorl in most cases. The embryonic shell is densely sculptured with prominent, close-set, rather evenly spaced, raised spiral striae (Figs. 5, 6). There are 4 of these striae per 0.1 mm, and each measures about 0.01 mm in transverse thickness and are perhaps about as high. Branching off the spiral striae are small diagonal spurs, close-set and coming off at more or less regular intervals. Most of these spurs terminate in the flat grooves or valleys that lie between adjacent parallel spiral striae. However, some of the spurs continue across to meet the adjacent spurs from the next stria, thereby forming crescent-shaped connections between the 2 striae (see Fig. 5). When a series of these cross-connections line up between a number of adjacent spiral striae, they form transverse striae. The spiral striae continue onto the neanic whorl, but rapidly become noticeably less prominent, although vestiges of them are clearly evident on the rest of the whorls. However, on the rest of the shell, transverse ribs are the dominant shell sculpture. These transverse ribs actually take their beginnings on the embryonic shell after about 1/2 whorl.

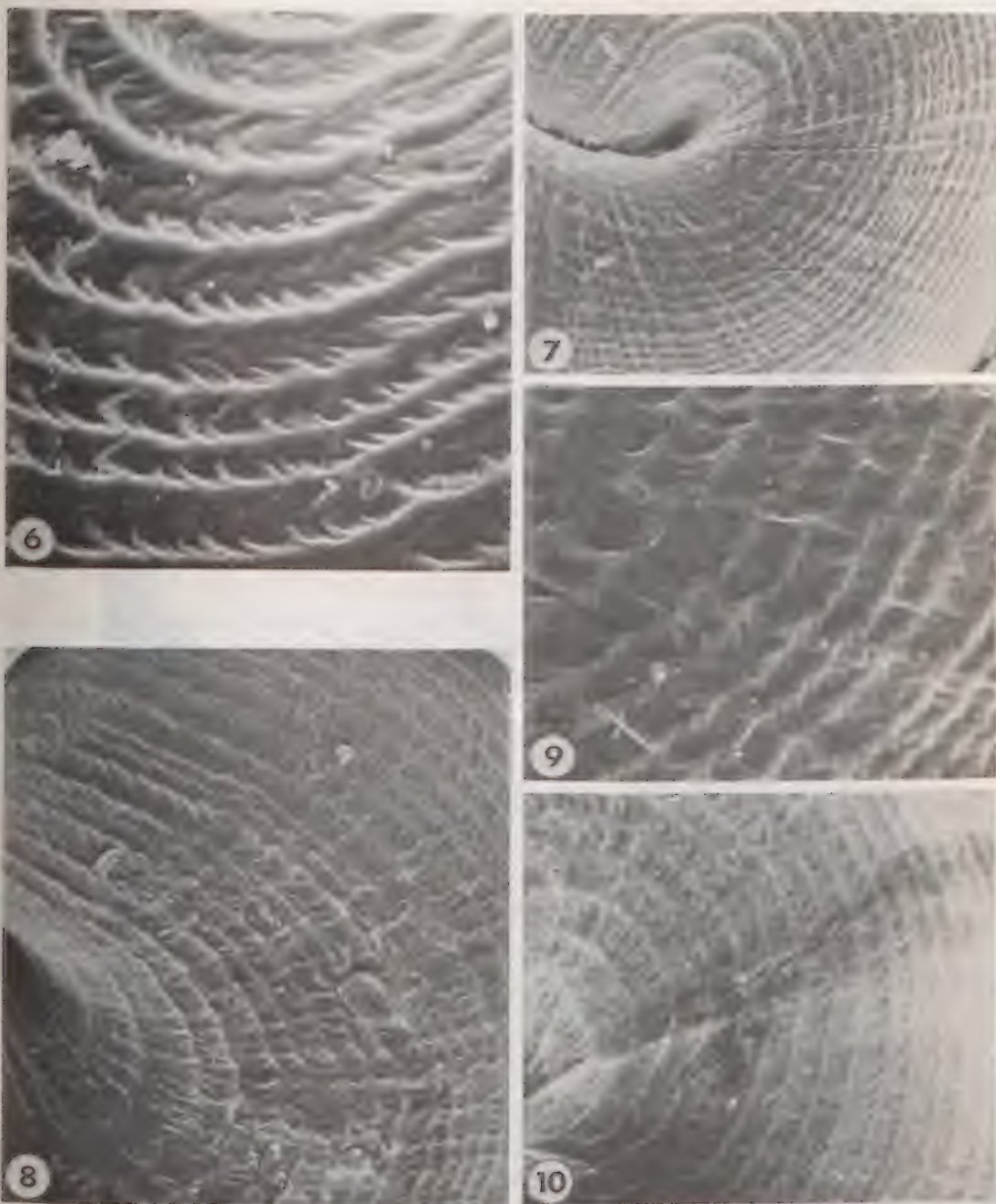
Valvata relicta. The embryonic shell surface sculpture (Figs. 7-9) of this species appears to be practically identical to that of *V. hirsutecostata* described above. However, the spiral striae are prominent for 2 whorls. The carina on the spire side of the shell begins a little past the first whorl, so presumably the neanic whorl begins at or prior to that point. A few low, irregularly spaced transverse ridges begin at the end of the first whorl. But, before the end of the first 1 1/2 whorls, these either cease or are obscured by the roughness of the growth lines.

Valvata tricarinata perconfusa. The surface sculpture of the embryonic shell of our specimens of this species is like that of the 2 *Valvata* species described above in all basic details, except that the ridges of the spiral striae are not quite as



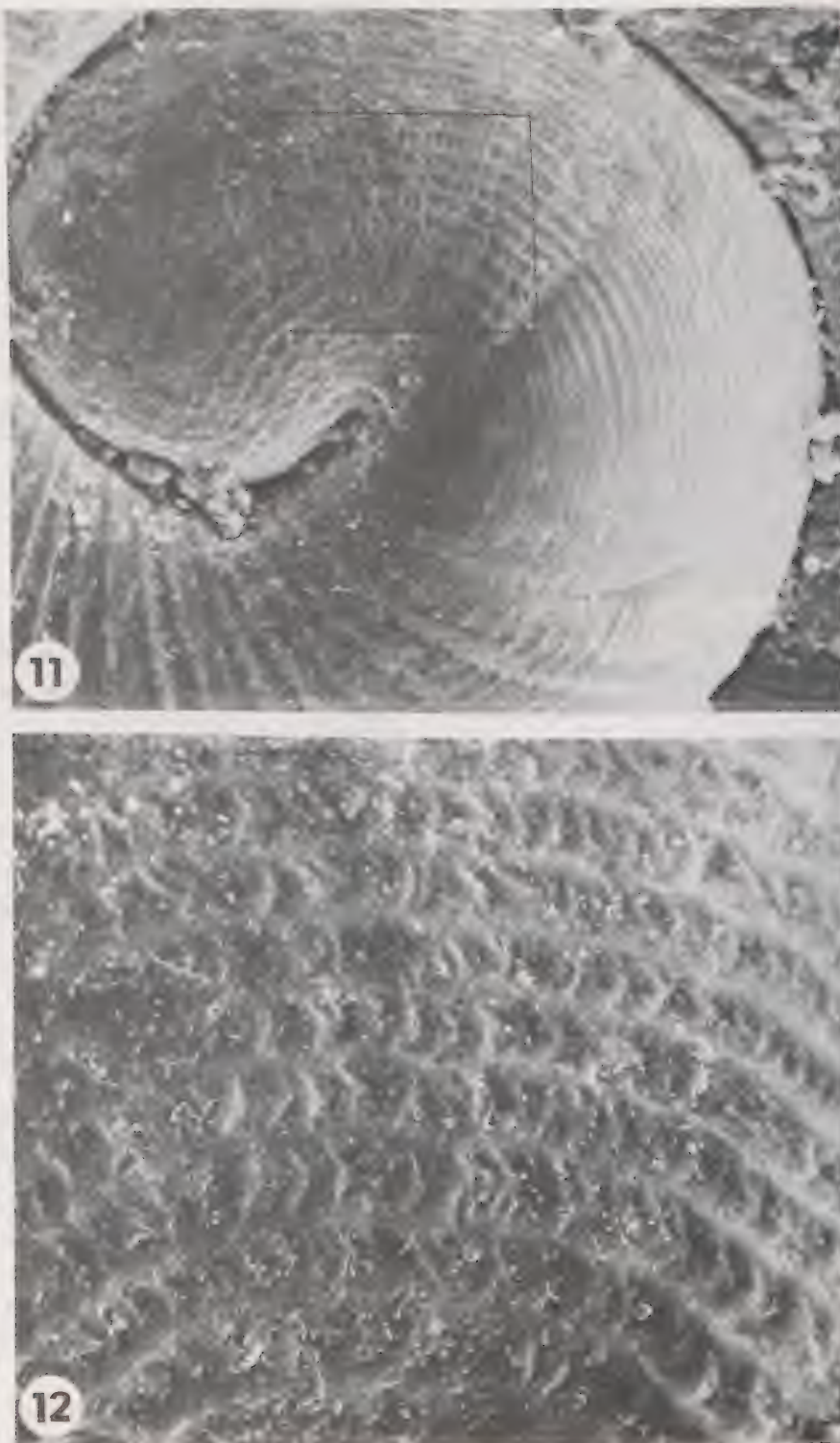
FIGS. 2-5. SEM photographs of the nuclear whorls of (Figs. 2-4) *Gocea ohridana* and (Fig. 5) *Valvata hirsutecostata*. Fig. 4 is an enlargement of the area marked in Fig. 3. Approximate magnifications: Fig. 2 - X215; Fig. 3 - X430; Fig. 4 - X860; Fig. 5 - X215.

prominent. The embryonic shell, almost exactly 1 whorl on all specimens observed, is set off from the rest of the shell by a distinct growth rest. The embryonic whorl is noticeably and distinctly striate, the striae continuing prominently on to the first neanic whorl for $1/2$ turn, and then ceasing for the most part. Low,



FIGS. 6-10. SEM photographs of the nuclear whorls of *Valvata hirsutecostata* (Fig. 6), *V. relictata* (Figs. 7-9) and *V. tricarinata perconfusa* (Fig. 10). Fig. 6 is an enlargement of the area marked in Fig. 5; Fig. 9 is an enlargement of the area marked in Fig. 7. Approximate magnifications: Fig. 6-X704; Fig. 7-X211; Fig. 8-X422; Fig. 9-X704; Fig. 10-X422.

rather regularly spaced transverse ridges start at the beginning of the second whorl and continue for $1/2$ to 1 whorl before losing their distinctness (perhaps ceasing or simply being obscured by the more prominent growth lines).



FIGS. 11, 12. SEM photographs of the nuclear whorl of a Pleistocene fossil shell of *Valvata humeralis*. Fig. 12 is an enlargement of the area marked in Fig. 11. Approximate magnifications: Fig. 11 - X300; Fig. 12 - X1000.

Valvata humeralis. The Pleistocene specimens we observed were all somewhat worn, but nevertheless the spiral surface sculpturing characteristic for the other 3 species of *Valvata* could be clearly discerned on the embryonic whorls of these fossil shells (Figs. 11–12). The sculpturing, although with less prominently high spiral striae, was basically the same as observed in the other 3 valvatid species. However, there is a much greater tendency for the spurs to connect completely between the adjacent parallel ridges of the striae (Fig. 2). The embryonic portion is set off from the rest of the shell by a growth rest occurring at 3/4 whorl to nearly 1 whorl. The spiral striae are prominent for 1 whorl, then they fade. (On the figured specimen [Fig. 11] there is a worn spot at the 3/4 whorl area.) Rather evenly spaced transverse ridges begin at 3/4 whorl to 1 whorl, and on some specimens these ridges continue for only another 1/2 whorl, but more commonly they go considerably farther, often continuing all the way to the apertural lip.

DISCUSSION

The sculpture of the nuclear whorls of *Valvata* as seen by the light microscope has been described previously. For example, for *V. tricarinata* Say, Baker (1928: 11) says, "nucleus . . . heavily, spirally striated or ridged; these ridges end abruptly and are separated from the following whorls by a distinct vertical ridge; for the next half turn there are both heavy spiral lines and heavy, spaced, vertical ridges, after which the growth lines remain distinct, rather crowded, and the spiral lines become very faint, but may be seen under high powers, even on the carinae." In the same work (p 23, 27) Baker described a similar sculpture for *V. sincera* Say and *V. lewisi* Currier, and Morrison (1940) mentioned the striate apex of *V. utahensis* Call, as did Kuiper (1947) for *V. piscinalis*. Binder (1967) studied 11 species of *Valvata* with the light microscope (*V. cristata* Müller, *V. piscinalis* (Müller), *V. macrostoma* Steenbuch and *V. naticina* (Menke) of Europe; *V. tricarinata* (Say), *V. sincera* Say and *V. virens* Tryon of America; *V. nilotica* Jickeli of Egypt; *V. baicalensis* Gerstfeld and *V. grubii* Dybowski of Lake Baikal; and *V. biwaensis* Preston of Japan). He described the basic sculpture as follows. "... La coquille embryonnaire des *Valvata* . . . est formée d'un demi-tour de spire replié en forme de U; elle est mal délimitée, sa surface est ornée de stries longitudinales (spirales) serrées, régulières, qui se prolongent parfois sur le début de la coquille post-embryonnaire. Les stries transversales de croissance n'apparaissent qu'après la fin de la coquille embryonnaire." And further, "En conclusion, on trouve une coquille embryonnaire caractéristique chez toutes les espèces que j'ai pu examiner et dont on est certain, grâce à leur anatomie, que ce sont bien des Valvatidae. On peut en inférer sans trop de risque qu'il s'agit là d'un caractère propre à toute la famille."

With the SEM, we could observe only to a very limited extent the spiral lines on the neanic and ephebic whorls; however, the sculpturing of those whorls does not concern us here. Of prime interest is the sculpturing of the embryonic shell, which seems quite distinct and characteristic for the Valvatidae, each species having the same basic pattern. In every specimen observed in our study, the surface sculpture consisted of a series of parallel, rather evenly spaced prominent spiral striae, each of the striae having secondary oblique side spurs, some of which had formed with crescent-shaped transverse connections with adjacent striae. The widths of the striae and of the intervening furrows between them were rather constant among the 4 species. Thus, the embryonic shell surface sculpture seems to be a constant and conservative morphological character in the Valvatidae, occurring in both Europe and the Western Hemisphere, and on both Recent and fossil shells. Binder

(1967) came to essentially the same conclusion from his observations with the light microscope.

The fact that *Gocea ohridana* has a quite basically different embryonic shell sculpture would seem to indicate that it is not a member of the Valvatidae as advocated by Radoman. Since there are no other SEM studies to our knowledge on the embryonic shell sculpture of freshwater prosobranch snails, we cannot at this time adequately compare *Gocea* to species of other families to which it may be related. A study of other members of the rissoacean family Hydrobiidae may prove especially interesting, since the radular characteristics and gross anatomy of *Gocea* indicate that it probably is a hydrobiid.

Robertson (1971) described the shell surface sculpture of the planktonic larvae of 6 species of marine gastropods (1 archaeogastropod and 5 mesogastropods). Of interest to our study is the nearly identical embryonic shell sculpture of *Gocea* and 3 of the species he studied, the cerithiaceans *Litiopa malanostoma* Rang and *Alaba incerta* (Orbigny), and the cypraeacean *Pedicularia decussata* Gould. In regard to *L. malanostoma* and *A. incerta* he says, "The SEM shows at high magnification that both species have an embryonic whorl with distinctive microsculpture, pits and minute granulations (Plate 4, Figures 13-15). The pits are irregularly positioned (in places fused), circular or polygonal, and most of them are between 1.0 and 1.5 microns in diameter; the intervening crests vary in width and height. The whole surface is minutely granulated, the granules being in the order of 0.1 to 0.2 micron in diameter and tending to be aligned." For *P. decussata*: "The embryonic shell surface is pitted except near the beginning of the suture and towards the growth line, where it is nearly smooth. The pits are nearly circular (commonly fused) and have radiating grooves; the pits increase in size away from the smooth areas; the larger pits are 3 to 4 microns in diameter (Plate 8, Figures 30-31). These embryonic shell pits are reminiscent of those of *Litiopa*, but *Pedicularia* has larger pits and a less granulate surface . . .". Concerning the similarities in embryonic shell sculpture between these seemingly "widely unrelated" genera, Robertson says, "The grossly similar embryonic shell microsculpture of *Litiopa* and *Pedicularia* seems attributable to similar internal shell structure - probably vertical crystalline rods that outcrop as pits and granular crests."

The basically identical embryonic shell microsculptural pattern observed for the mesogastropods *Gocea* (superfamily Rissoacea), *Litiopa* and *Alaba* (superfamily Cerithiacea), and *Pedicularia* (superfamily Cypraeacea) may be fortuitous and of no phylogenetic significance, as Robertson suggested for the species he studied, the similar patterns simply being the result of the same underlying shell structure, which in itself may not relate to common ancestry. But, inasmuch as so little is known of the embryonic shell sculpture of other mesogastropods, such a contention at present is at best quite speculative.

ACKNOWLEDGEMENTS

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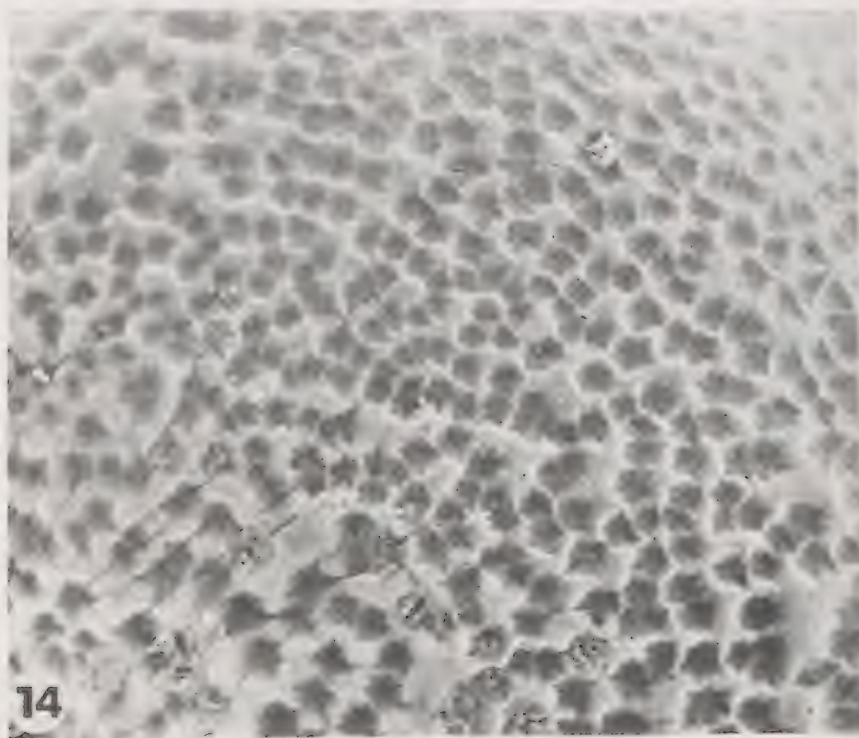
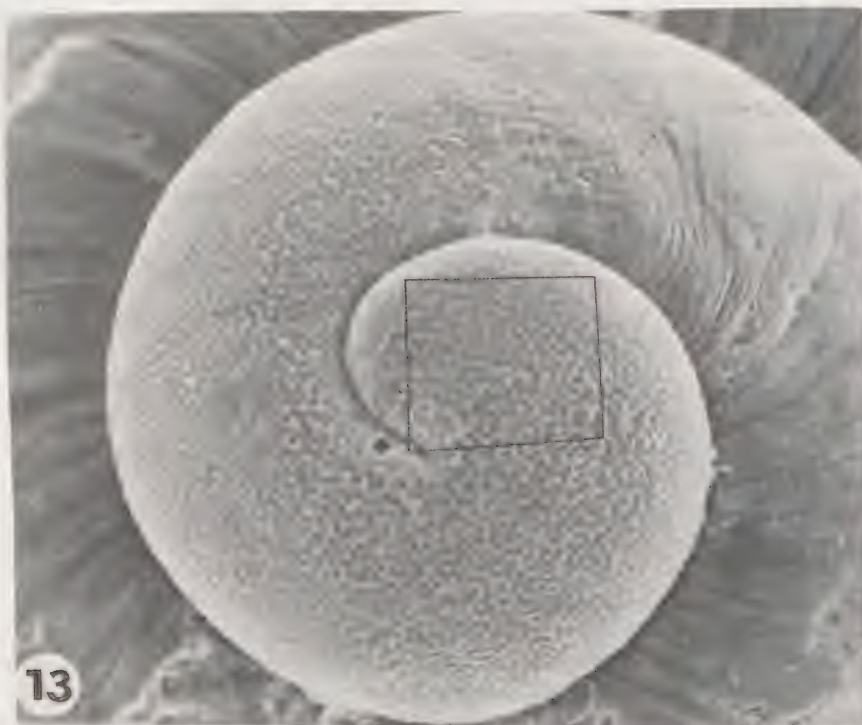
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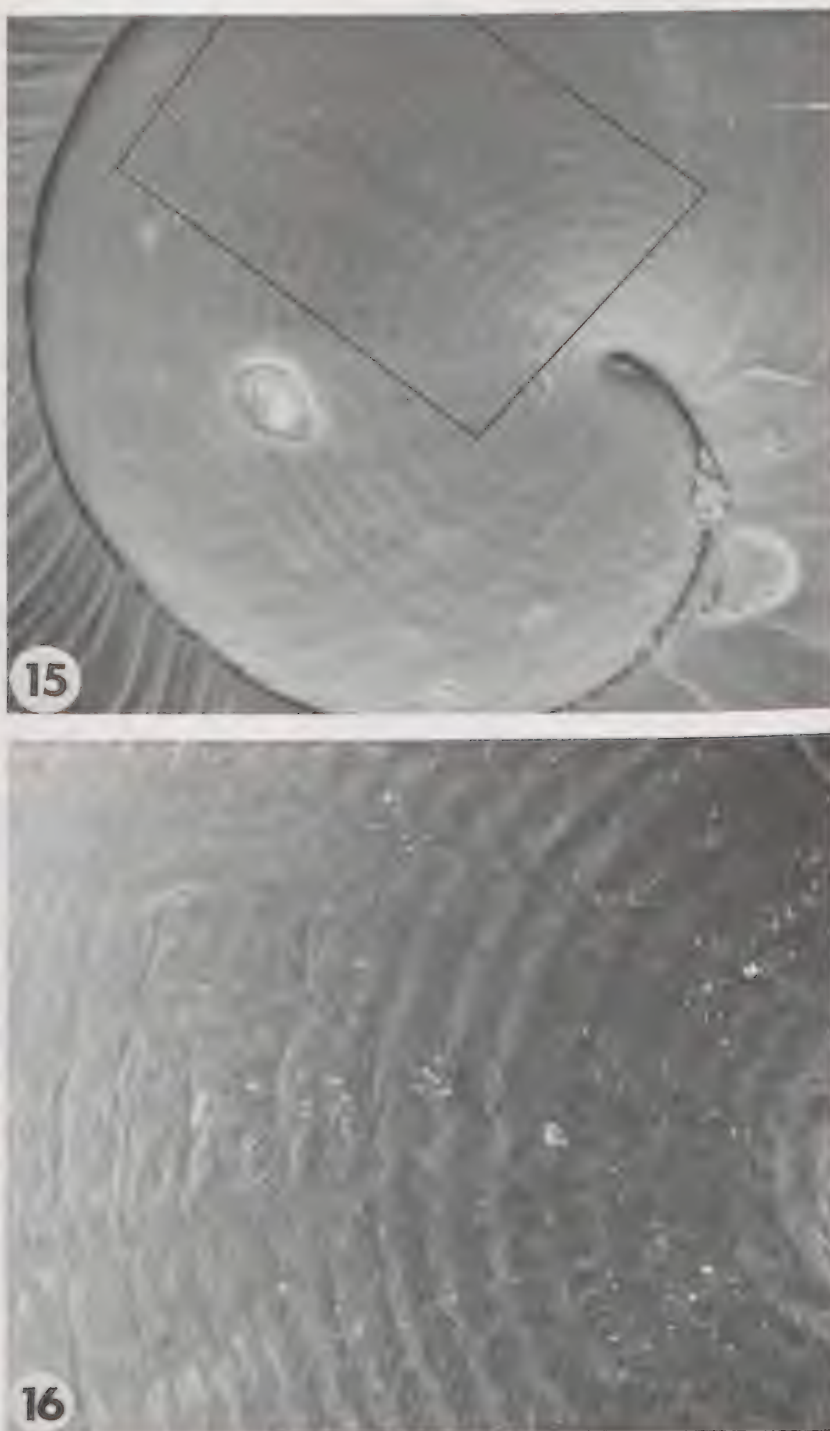
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ADDENDUM

After the preceding article was written, we were able to study the Lake Ohrid hydrobiid *Ohridohoratia pygmaea* (Westerlund) (collected from the littoral zone at Odejče), as well as 2 additional species and a subspecies of *Valvata*. The valvatids were *Valvata sincera sincera* Say from Rockport, Knox Co., Maine, U.S.A. (UMMZ 28642); *V. sincera onlariensis* (Baker) from Crooked Lake, Lennox and Addington Co., Canada (UMMZ 231780); and *Valvata (Megalovalvata) baicalensis* Gerstfeld of Lake Baikal, Siberia (UMMZ 51901). The significance of studying the apical microsculpture of these 3 valvatid taxa is that each of them contains partially uncoiled shells similar in gross appearance to the shell of *Goea ohridana*.



FIGS. 13, 14. Apical shell sculpture of *Ohridohoratia pygmaea*. Approximate magnifications: Fig. 13 - X300; Fig. 14 - X1000. Fig. 14 is an enlargement of the area marked in Fig. 13.



FIGS. 15, 16. Apical shell sculpture of *Valvata sincera sincera*. Approximate magnifications: Fig. 15 - X300; Fig. 16 - X600. Fig. 16 is an enlargement of the area marked in Fig. 15.



FIG. 17. Apical shell sculpture of *Valvata baicalensis*. Approximate magnification: X600.



FIG. 18. Radular teeth of *Cocea ohridana*. Approximate magnification: X6880. C = central teeth; L = lateral teeth; M = marginal teeth; b = basocone; m = mesocone; ec = ectocone; en = entocone. This photograph and the one in Fig. 19 were taken by Dr. Alan Solem.



FIG. 19. Radular teeth of *Gocea ohridana*. Approximate magnification: X5310. See legend to Fig. 18 for key to labels.

The apical microsculpture of *Ohrdohoratia pygmaea* is shown in Figs. 13 and 14. It seems to be identical with that shown in Figs. 2 and 3 for *Gocea ohridana*. The shallow pits which pockmark the embryonic shell surface are the same in size, shape, arrangement and density. The only apparent difference between *G. ohridana* and the specimen of *O. pygmaea* is that the cessation of the pitted sculpture is not as abrupt on the latter.

The apical microsculpture of *Valvata sincera sincera*, *V. sincera ontariensis* and *V. baicalensis* have the characteristic spiral and transverse ridges of the previously studied *Valvata* species. Our subadult shell specimens of *V. sincera sincera* and *V. sincera ontariensis* (the latter subfossils) were rather worn, but the pattern of the apical sculpture was nevertheless quite evident. The 1 subadult specimen of *V. baicalensis* we studied was apparently live when collected, but nevertheless was also somewhat worn (and heavily eroded in places). Fig. 17 shows the parallel spiral striae with lower adjoining parallel transverse ridges.

Further, we have SEM photographs of the radular teeth of *Gocea ohridana*, kindly taken by Dr. Alan Solem (Figs. 18 and 19). These photographs show in greater detail the tooth characteristics already shown by Hadžišć (1956: fig. 3). The mesocone of the central tooth is hardly larger than the flanking ectocones, but on the lateral teeth the mesocones are considerably longer than the entocones and ectocones. The cusps of the marginal teeth are mostly equal in size. In Fig. 18 can be seen the basocone cusps of the central tooth, characteristic of hydrobiids, but lacking in the valvatids.

These additional observations augment our previous ones on *Gocea* and *Valvata* and strengthen our contention that *Gocea* is not a member of the Valvatidae, but is probably a hydrobiid, as the senior author originally contended.

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ANATOMICAL SYSTEMATICS OF *ETHERIA ELLIPTICA*
(PELECYPODA: MYCETOPODIDAE)

William H. Heard and Virginia A. Vail

ABSTRACT

Gross dissection and histological examination of preserved *Etheria elliptica* from Africa revealed this species to be most closely related to the Neotropical Mutelacea: Mycetopodidae, and not to the Unionacea or to the Ethiopian Mutelacea: Mutelidae with which it was hitherto customarily classified. Etheriidae Swainson 1840, for which *E. elliptica* is the type, is placed in synonymy of Mycetopodidae Gray 1840. This is the first interpretation of a species of one mutelacean family occurring in a disjunct biogeographic region to which members of the other family are restricted.

INTRODUCTION

The nominal family Etheriidae Swainson 1840 is generally considered to comprise 4 monotypic nominal genera: (1) *Etheria* Lamarck 1807 [type species by subsequent designation by Gray (1847): *E. semilunata* Lamarck 1807: 404 (= *E. elliptica* Lamarck 1807: 401)], in the Senegal, Niger, Congo and Nile drainages in continental Africa and also from the Malagasy Republic (Madagascar), (2) *Acostaea* d'Orbigny 1851 [type by monotypy: *A. guaduasana* d'Orbigny 1851 (= *Mulleria rivoli* Deshayes 1827)], in the Rio Magdalena in Colombia, (3) *Bartlettia* H. Adams 1866 [type by monotypy: *Etheria stefanensis* Moricand 1856], in the Amazon drainage in Brazil, Peru and Ecuador, and the Paraguay basin in Paraguay, and (4) *Pseudomulleria* Anthony 1907 [type by monotypy: *Mulleria dalyi* E.A. Smith 1898], in the Budra drainage in the State of Mysore in southwestern India.

Whereas some authors (e.g., Pilsbry & Bequaert, 1927; Thiele, 1935; Haas, 1936, 1969a, 1969b; Pain & Woodward, 1961; Yonge, 1962; Parodiz & Bonetto, 1963) have recognized these freshwater bivalves as a distinct, natural family with affinities to the Unionacea: Unionidae s.l., others have considered this assemblage to represent groups in the Mutelacea: Mutelidae s.l. Modell (1942) placed *Bartlettia* and *Acostaea*, and *Etheria* and *Pseudomulleria* in his new mutelid subfamilies Bartlettiinae and Etheriinae, respectively, and Mandahl-Barth (1954, 1968) considered *Etheria* to be a monotypic but highly variable, transformed mutelid genus. In a recent classification, Morrison (1973) created the new familial taxa Acostaeidae and Pseudomulleriidae; *Etheria* was retained in the Etheriidae. He considered *Acostaea*, *Bartlettia* and *Etheria* to be mutelaceans and included *Pseudomulleria* with the Unionacea. Morrison's views are in contrast to those of Haas (1969a, 1969b), who recorded *Pseudomulleria* as a subgenus of *Acostaea* and recognized Unionacea as the sole superfamily of freshwater mussels.

Etheriids were originally grouped together on the basis of their peculiar shell forms, which in adults are unlike those of other naiades. Yonge (1962) subsequently recorded that they share another feature unique among naiades: owing to a localized transverse "pinching," the posterior outer ligament layer is compressed and extended to a corresponding extent laterally into the valves. Petit de la Saussaye (1853), Anthony (1905, 1907), Pain & Woodward (1961), Yonge (1962) and Haas (1969a) provided detailed shell descriptions and/or taxonomic characterizations of these

naiades. Differences between the 4 species, both in shell and animal features, are listed in Table 1.

TABLE 1. Characterization of adult and larval etheriid and other naiades.¹

Feature	"Etheriidae"				Mutelacea	Unionacea
	<i>Acostaea</i> ²	<i>Bartlettia</i> ²	<i>Etheria</i>	<i>Pseudomulleria</i>		
Inequivalved	+	-	+	+	-	-
Adults sessile	+	-	+	+	-	-
Adductor muscles						
Monomyarian	+	-	-	+	-	-
Dimyarian	-	+	+	-	+	+
Posterior mantle						
"Openings"	?	?	+	+	+	+
True siphons	?	?	-	-	+	-
Foot present	?	?	-	-	+	+
Demibranchs						
Plicate	?	?	+	-	-	-
Non-plicate	?	?	-	+	+	+
Marsupium						
Endobranchous	?	?	+	?	+	-
Exobranchous	?	?	-	-	-	+
Tetragenous	?	?	-	-	-	+
Larval type						
Glochidium	?	?	?	?	-	+
Lasidium or lasidium-like	?	?	?	?	+	-

¹+ indicates presence of a feature, - indicates its lack.

²Animal unknown.

According to Heard & Guckert (1970) and Heard (1974), different anatomical organizations offer significant characters for interpretation of phylogenetic affinities of naiades at the subfamilial and familial levels. The anatomy of *Etheria elliptica* was previously described by Rang & Cailliaud (1834), Anthony (1905, 1907), Sassi (1910) and Yonge (1962), and that of *Pseudomulleria dalyi* by M.F. Woodward (1898), but the animals of *Acostaea rivoli* and *Bartlettia stefanensis* are as yet unknown.

Several significant features were overlooked in previous anatomical accounts of *Etheria elliptica*. The purposes of this report are the description of those features, confirmation of other attributes already noted, and a revised higher classification of this species.

MATERIAL EXAMINED

In this section is detailed the date, locality and other information on the *Etheria elliptica*

studied here. Shells of these animals have been deposited in the Museum of Zoology, University of Michigan (UMMZ). A list of other taxa whose animal anatomies have personally been studied for comparison is included.

Etheria elliptica

(1) One male from Lake Victoria at Entebbe, Uganda; 26 January 1951. UMMZ 234708. Right valve (Fig. 1) concave, larger: 38.6 mm long x 36.2 mm high; left valve (Fig. 2) convex, smaller (35.3 x 35.3 mm), formerly attached to a solid substrate across its anterior half. (2) One gravid female from the Laupula River above Johnston Falls, Katanga Province, Zaire; 22 December 1959. UMMZ 234709. Left valve (Fig. 3) convex, 76.2 x 60.7 mm, with a prominent "beak" directed dorsoanteriorly; right valve (Fig. 4) flattened, 77.7 x 58.3 mm, formerly narrowly attached to a solid substrate at the anterior end, lacking a "beak."

Other Naiades Examined

Mutelacea: Mutelidae Gray 1847 (restricted to the Ethiopian Region by Parodiz & Bonetto, 1963). *Aspatharia (Spathopsis) petersi* (von Martens), *A. (S.) wahlbergi* (Krauss), *Mutela alata* (Lea), *M. bourguignati* Bourguignat and *M. nyassaensis* (Lea).

Mutelacea: Mycetopodidae Gray 1840 (Neotropical Region, *fide* Parodiz & Bonetto, 1963). *Anodontites trapesialis* form *exotica* (Lamarck).



FIGS. 1-4. Shells of *Etheria elliptica*. FIG. 1. Inner surface of right valve of Lake Victoria male. FIG. 2. Outer surface of left valve of Lake Victoria male. FIG. 3. Outer surface of left valve of Laupula River female. FIG. 4. Inner surface of right valve of Laupula River female. A, anterior; D, dorsal. See text page 17 for sizes.

Unionacea: Amblemidae Rafinesque (Palearctic, Ethiopian, Oriental and Nearctic regions, *fide* Heard, 1974). *Caelatura framesi* (Connolly) and *C. hypsipryma* (von Martens) from Africa, *Pilsbryconcha exilis* (Lea) and *Pseudodon cambodjensis* (Petit de la Saussaye) from southeastern Asia, and *Megalonaias boykiniana* (Lea) and *Plectomerus dombeyanus* (Valenciennes) from North America.

Unionacea: Hyriidae Swainson (Australian and Neotropical regions, *fide* Parodiz & Bonetto, 1963). *Hyridella australis* (Lamarck) from Australia.

Unionacea: Margaritiferidae Haas (Palearctic and Nearctic regions, *fide* Heard & Guckert, 1970; Heard, 1974). *Margaritifera falcata* (Gould) from North America.

Unionacea: Unionidae Rafinesque (Palearctic, Ethiopian, Oriental and Nearctic regions, *fide* Heard, 1974). *Anodonta* spp. (cf. Heard, 1975), *Elliptio crassidens* (Lamarck), *Lampsilis claibornensis* (Lea) and *Villosa vibex* (Conrad) from North America, *Cafferia caffra* (Krauss) from Africa, and *Physunio eximius* (Lea) and *Uniandra contradens tumidulus* (Lea) from southeastern Asia.

METHODS

Gross dissection provided for the description of general anatomical features. Histological examination (material prepared as by Heard, 1975) was employed to ascertain the sex of the individuals and to determine the structural details of the demibranchs.

ANATOMICAL FINDINGS

General features

Animals conspicuously dimyarian (cf. Yonge, 1962: fig. 3 on p 428). Mantle sheets united posteriorly only directly behind the ctenidia. True siphons absent, with only an excurrent (anal) and an incurrent (branchial) opening present above and below the mantle fusion, respectively; excurrent opening unclosed above (i.e., pallial suture separating the excurrent opening from a distinct supra-excurrent opening is lacking), and pedal slit continuous with the incurrent opening. Foot entirely lacking. Labial palpi relatively short and of low height for the size of the animal, with their base nearly contiguous with the anterior end of the inner demibranchs. Two ctenidia present, each comprising an outer and an inner demibranch. Outer demibranchs of equal size in each animal, and up to 2 mm shorter than the inner demibranchs which are also of equal size. Diaphragm formed by the dorsal margins of the ctenidia and the mantle fusion between the excurrent and incurrent openings, complete and entirely separating the branchial and suprabranchial chambers.

Both specimens with a narrow band of densely concentrated melanin pigment along the inner edge of the mantle. Male with a single row of short, conical papillae at the apical margin of the inner edge of the mantle from the level of the anterior adductor muscle through the upper 2/3 of the excurrent opening; female similar, but lacking papillae along the excurrent opening. Other, more striking and significant sexually dimorphic features occur in the demibranchs.

Demibranchs

Outer demibranchs in both specimens with the outer (ascending) lamella dorsally attached to the inner surface of the mantle for its entire length, and with the inner (descending) lamella dorsally joined to the dorsal margin of the outer (descending) lamella of the inner demibranchs. Dorsal margin of the inner (ascending) lamella of the inner demibranchs united to the visceral mass along the length of the latter and, posterior to the visceral mass, to the dorsal margin of the inner lamella of the apposing inner demibranch. Outer and inner lamella of each demibranch of



FIGS. 5-8. Photomicrographs of frontal sections of lamellae of *Etheria elliptica*. FIG. 5. Exposed plicae of outer lamella of male inner demibranch. FIG. 6. Protected plica of inner lamella of male outer demibranch. FIG. 7. Protected plica of dorsal region of outer lamella of female inner demibranch. FIG. 8. Exposed plica of ventral region of outer lamella of female inner demibranch. CC, cellular covering; E, embryo; PL, plica; S, septum; VR, vertical ridge; WT, water-tube. Scale for all figures: 200 μ .

equal height, with those of the inner demibranchs higher than those of the outer demibranchs.

All 4 demibranchs in each specimen vertically plicated. Plicae of male inner demibranchs (Fig. 5) and of female outer demibranchs exposed; inner lamella plicae of male outer demibranchs protected by a cellular covering (Fig. 6), as dorsally (Fig. 7) but not ventrally (Fig. 8) are the outer lamella plicae of female inner demibranchs. All 4 demibranchs in each sex with 2 plicae on either side of every water-tube, and interlamellar junctions (i.e., septa) at alternate interplicate positions (Fig. 9). Male inner demibranch lamellae with a few more filaments per plica than in the outer demibranchs (Table 2). Female with about the same number of filaments per plica in both lamellae of the outer demibranchs, in the inner lamella of the inner demibranchs and in the ventral, exposed region of the outer lamella of the inner demibranchs; latter with significantly fewer filaments per plica in the dorsal, protected region.

Each demibranch in both sexes with ordinary (Fig. 9: OF) and principal filaments (PF). All filaments possessing fine frontal (Figs. 10, 11: FFC), coarse frontal (CFC) and latero-frontal cilia (LFC).

TABLE 2. Numbers of filaments per plica of different lamellae of *Etheria elliptica* (values based on 10 plicae per lamella).

Lamella	Male $\bar{x} \pm \sigma$	Female $\bar{x} \pm \sigma$
Inner demibranch		
Inner lamella	14.3 ± 0.9	15.4 ± 1.6
Outer lamella	13.5 ± 2.0	$9.5 \pm 1.6^*$ $15.0 \pm 0.8^\dagger$
Outer demibranch		
Inner lamella	11.7 ± 1.8	15.0 ± 1.3
Outer lamella	12.1 ± 0.7	14.7 ± 1.1

*Dorsal region, protected by a cellular membrane.

†Ventral, exposed region.

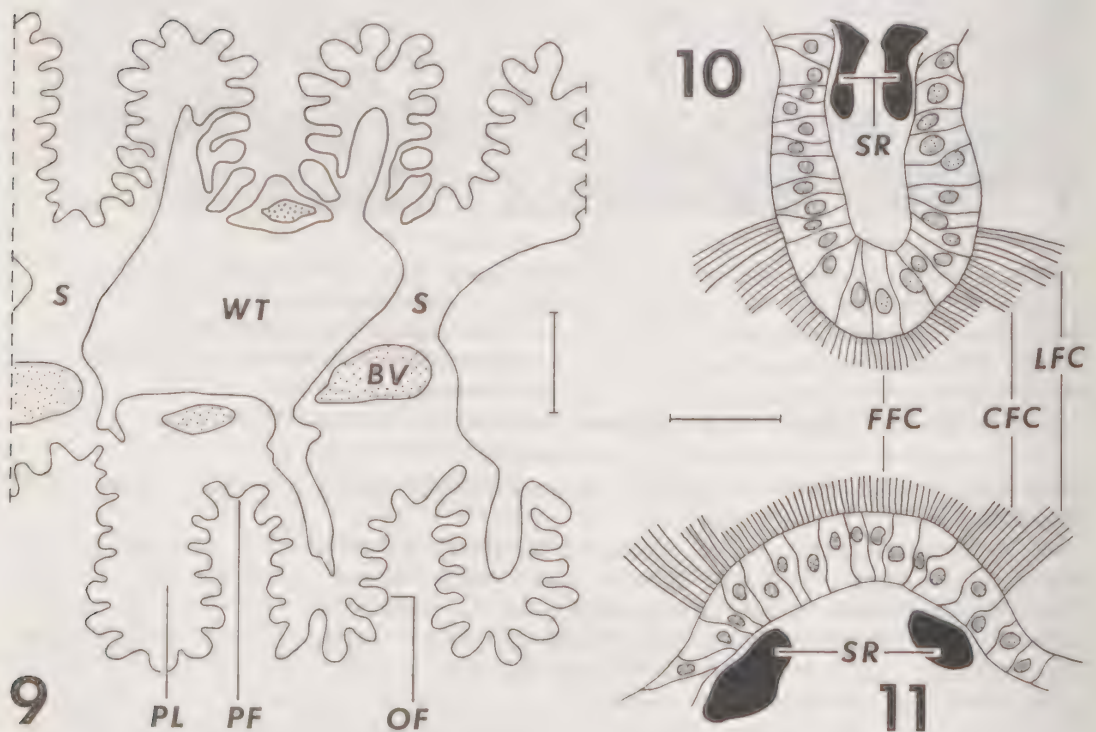


FIG. 9. Frontal aspect of part of a non-marsupial demibranch. BV, blood vessel; OF, ordinary filament; PF, principal filament; PL, plica; S, septum; WT, water-tube. Scale: 250μ .

FIGS. 10, 11. Transverse views of an ordinary (Fig. 10) and a principal filament (Fig. 11). CFC, coarse frontal cilia; FFC, fine frontal cilia; LFC, latero-frontal cilia; SR, supporting rod. Scale: 25μ .

Interlamellar junctions developed as continuous, uninterrupted primary septa (Fig. 9: S), with those in the male outer demibranchs only 4/5 as high as the lamellae; septa in the male inner demibranchs and in all female demibranchs of the same height as the lamellae. Primary septa in female inner demibranchs with faint traces of 3 possibly fused perforations. Inner demibranchs of female also possessing, adjacent to the outer lamella, a vertical ridge of tissue projecting into consecutive water-tubes from each surface of the primary septa (Figs. 7, 8: VR).

Endobranchous, i.e., only the inner demibranchs marsupial, and in these the developing young in the gravid female occurred just in the central 3/5 of the length of the demibranchs. Only embryos present. Diameter of fertilization membrane: 77 μ ; diameter of embryos: 65 μ .

DISCUSSION

The present findings agree with those of prior accounts on *Etheria elliptica*, except that (1) Rang & Cailliaud (1834) failed to record a posterior mantle union behind the ctenidia, described the ctenidial plicae as tubes and noted the presence of a large foot, (2) Anthony (1905, 1907) illustrated perforated septa in all 4 demibranchs of a non-gravid animal of unstated sex but did not mention these perforations in the text description, and (3) Yonge (1962: 432) stated that the ctenidial "axes are free for the posterior quarter of their length." In addition, Sassi's (1910: 30) contention that "Ausserdem sind grosse Teile der beiden Mantellappen mit Gonaden erfüllt," and his suggestion of the presence of a reduced anterior byssal gland, were not confirmed in this study. Finally, all prior workers overlooked the cellular cover protecting the plicae of certain lamellae, and none noted the presence of what may be incipient secondary septa emanating from each primary marsupial septum. In fact, Anthony's (1905, 1907) illustration of a frontal section of a gravid marsupial demibranch does not include those vertical ridges of tissue.

Etheria elliptica is endobranchous, a feature common to the Unionacea: Hyriidae and to the Mutelacea: Mutelidae and Mycetopodidae. Its mature larvae are unknown, and direct evidence of its superfamilial membership is lacking. However, indirect evidence is provided by comparisons of anatomical attributes, i.e., evidence of familial membership.

All 4 demibranchs in each sex of *Etheria elliptica* contain comparatively distantly spaced and at least sometimes (seasonally?) imperforate interlamellar septa. That condition is known elsewhere among naiades only in mutelaceans, although Germain (1909) illustrated perforated septa in the mutelid *Chelidonopsis arietina* (Rochebrune) [= *Mutela (Chelidonopsis) hirundo* (von Martens), *vide* Haas (1969a: 584)].

Distantly spaced but perforated septa occur in primitive, tetragenous Unionacea: Amblemididae, and both sexes of hyriids also contain perforated septa in all 4 demibranchs (Ortmann, 1912a, 1920, 1921; pers. observ.). However, hyriids, like unionids, display a dimorphic septal spacing: dense in the region of the marsupium and distant elsewhere (cf. Heard, 1974). Hyriids also differ from *Etheria elliptica* in possessing a continuous pallial suture without a supra-excurrent opening above the excurrent opening (South America) or siphon (Australia) (see Ortmann, 1912a, 1920, 1921; McMichael & Hiscock, 1958; Parodiz & Bonetto, 1963; pers. observ.).

Mutelids are distinguished from *Etheria elliptica* by the presence of true excurrent and usually also incurrent siphons, absence of branchial papillae except in the pseudotaxodont *Iridina spekii* (Woodward), attachment of the inner lamella of the inner demibranchs to the visceral mass only anteriorly, presence of a continuous pallial suture above the excurrent siphon, and the absence of vertical ridges on

marsupial septa (cf. Pelseneer, 1886; Germain, 1909; Ortmann, 1910a, 1918; Bloomer, 1932; Leloup, 1950; Pain & Woodward, 1968; also verified here).

Etheria elliptica shares with mycetopodids those anatomical features by which it is distinguished from mutelids: absence of true siphons and a pallial suture above the excurrent opening, presence of pallial papillae (but not true branchial papillae of other mycetopodids and all unionaceans) and also the vertical septal ridges in the marsupial demibranchs, and greater extent of attachment of the inner demibranchs to the visceral mass (cf. Ortmann, 1911, 1921; Parodiz & Bonetto, 1963; also personally verified).

Of special interest are the vertical septal ridges near the outer lamella of the marsupial demibranchs of *Etheria elliptica*. As noted, true mutelids lack them, whereas Ortmann (1921: 458, 566) recorded their widespread occurrence, also near the outer lamella of the inner demibranchs, in "female" mycetopodids. These ridges were also found in the present study in both inner and outer demibranchs of 6 animals of the mycetopodid *Anodontites trapesialis* f. *exotica* [= *A. exoticus* (Lamarck), *fide* Haas (1969a: 570)], each of which was a non-gravid hermaphrodite. Such ridges are unknown in the Unionacea (see Ortmann, 1910b, 1912b), although female and female-hermaphrodite Unionidae: Anodontinae possess a secondary septum adjacent to each lamella of the outer, marsupial demibranchs (Heard, 1975), and at least some Hyriidae possess several ridge-like projections on each side of marsupial septa (cf. McMichael & Hiscock, 1958: fig. 6 on p 379; Ortmann, 1921: fig. 2a in pl. 48).

Parodiz & Bonetto (1963) characterized the mutelacean Mycetopodidae and Mutelidae as distinct familial groups in part on the basis of larval type. The Neotropical mycetopodids produce lasidia (cf. von Ihering, 1891; Bonetto, 1951; Parodiz & Bonetto, 1963), and the Ethiopian mutelids generate lasidia-like larvae (viz., haustoria, *fide* Fryer, 1959, 1961). Although the mature larval type of the Ethiopian *Etheria elliptica* remains unknown, the adult anatomy of this species recommends its classification with the Neotropical Mutelacea: Mycetopodidae.

This action treats Etheriidae Swainson 1840 and Mycetopodidae Gray 1840 as synonyms. Acting as "first reviser" (Art. 24a, ICZN), we select Mycetopodidae Gray as the senior synonym.

Parodiz & Bonetto (1963) considered the Mutelidae and Mycetopodidae to be mutually exclusive geographically. The present findings indicate an exception, but such an intrafamilial disjunction may not be unique inasmuch as Bonetto (1963) and Parodiz & Bonetto (1963: 206-207) noted that the Neotropical "mycetopodid" *Leila blainvilleanus* (Lea) has siphons, several dorsal muscle scars in the shell and a *Mutela*-like (i.e., haustorium-like) larva; all are features of Ethiopian mutelids.

Whether the remaining 3 "etheriids" constitute a monophyletic group (disputed by Morrison, 1973; 1975, pers. comm.) is presently unknown because the animal of only *Pseudomulleria dalyi* has been described. Judged from Woodward's (1898) anatomical account, it appears to be a monomyarian mutelid and not a unionacean as suggested by Morrison (1973) on conchological grounds. In addition, the animal of *Bartlettia stefanensis* is as yet unknown, although Parodiz & Bonetto (1963) and Morrison (1973) considered the species to be a member of the mycetopodid genus *Anodontites* Bruguière.

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MOLLUSKS OF THE SHEYENNE RIVER,
NORTH DAKOTA, U.S.A.: PRESENT AND PAST

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ABSTRACT

The Sheyenne River, a tributary of the Red River in eastern North Dakota, is the longest river in the state and contains the greatest number of mollusks. Thirty-one species are known to inhabit the river: 12 mussels (unionacean bivalves), 6 pill clams (sphaeriid bivalves) and 13 snails (4 prosobranchs and 9 pulmonates). Sixteen species are known to occur in Lake Ashtabula (man-made reservoir in the middle reaches of the Sheyenne River): 4 mussels, 4 pill clams and 8 snails (3 are prosobranchs); and 7 species of mollusks (all pulmonate snails) were found in Sheyenne Lake (uppermost reaches of the Sheyenne River). Two snails, *Gyraulus circumstriatus* and *Aplexa hypnorum*, were found only in Sheyenne Lake. One pill clam (*Pisidium ntidum*) and 5 snails (*Valvata tricarinata*, *Cincinnatia cincinnatiensis*, *Amnicola limosa*, *Gyraulus parvus* and *Helisoma anceps*) occurred in greater densities in Lake Ashtabula than elsewhere. River discharge seems to be a primary factor in affecting mollusk occurrence in the Sheyenne River. Low or zero discharge relates to low mussel diversity and high discharge relates to high mussel diversity. Certain pill clams and snails seem to prefer flowing or stagnant (non-flowing) water. An unstable bottom (as one of rippled sand) seems also to primarily restrict mollusk occurrence. Other factors possibly limiting the occurrence of mollusks in the Sheyenne River are high turbidity (pill clams and snails), relatively high potassium (mussels) and lack of suitable fish host (mussels). The fossil molluscan fauna generally resembled the living fauna, but lacked 13 species (2 mussels, 4 pill clams and 7 snails). No fossil species were different from those living now, with the possible exception of the snail *Campeloma decisum*, whose present existence in the Sheyenne is uncertain. Mollusks inhabited the ancestral Sheyenne River that flowed into glacial Lake Agassiz at least as early as about 13,500 years ago, and the modern Sheyenne at least as early as about 2,500 years ago.

INTRODUCTION

Previous work and purpose

The Sheyenne River in eastern North Dakota is within the Hudson Bay drainage. This river is the longest in the state and has the greatest diversity of molluscan fauna. Little study, however, has been devoted to those mollusks of the river.

Coker & Southall (1915: 15) reported 4 species of mussels (unionacean bivalves) from the river at Lisbon. Winslow (1921: 10-16) listed 2 species of mussels, 6 species of pill clams (sphaeriid bivalves) and 9 species of snails (2 prosobranchs and 7 pulmonates) from the upper part of the river. Cvancara (1970) reported on the mussels from 5 stations in the lower part of the river. Peterka (1972) discussed 2 genera of pill clams and 4 genera of snails from Lake Ashtabula, a man-made reservoir on the river. Clarke (1973) reported 5 mussels, 1 pill clam and 1 snail from a single station in the lower part of the river. The only detailed study

of all mollusks of an entire river in North Dakota is that of Cvancara, Erickson & Delimata (1972). One of us (Cvancara, 1975) has recently summarized what is known of the aquatic mollusks in North Dakota.

Our report gives the distribution of mollusks of the Sheyenne River, evaluates the primary ecologic factors influencing their occurrence and compares the living mollusks with the fossil molluscan fauna associated with the river. This study should be useful in assessing the environmental impact of the in-progress irrigation Garrison Diversion Project on the Sheyenne River drainage.

Geologic setting and stream characteristics

Originating in central North Dakota (Sheridan County), the Sheyenne River generally flows east, south and northeast and joins the Red River of the North about 13 km north of Fargo (Fig. 1). It flows primarily through the undulating to hilly Drift Prairie, except for about the lower 1/4 of its length (below station 26), where it flows across the dominantly flat Red River Valley. The river flows in a trench cut during the late Quaternary when meltwater flowed southeastward from glacial Lake Souris to glacial Lake Agassiz (Aronow, 1963).

The bottom sediment is determined by the glacier- and glacial lake-related sediments and shales of Late Cretaceous age through which the river cuts. From station 2 to about station 26, the river is cut into bouldery sand, silt and clay (glacial till; forms ground and end moraine), sand and gravel (glacial meltwater deposits; form outwash plains), and marine shales, exposures of which are common from about station 12 to station 25 (Bluemle, 1965, 1973; Bluemle et al., 1967; Bluemle, unpubl. map of Ransom County; Carlson & Freers, 1975; Kelley & Block, 1967; Merritt, 1966; and Rude, 1966). Above station 26, the bottom sediment is mostly pebbly sand and sandy pebble gravel (Table 2). Shale is common to abundant in the coarser particles at many places. From below station 26 to about station 29, the Sheyenne cuts into sand and silt associated with the glacial Sheyenne delta (Baker, 1967). Within the area of the delta, the bottom sediment is primarily well-sorted sand. From below station 29 to the mouth, the river cuts into silt and clay of the plain of glacial Lake Agassiz (Klausing, 1968); here, the bottom sediment is muddy sand and mud.

The Sheyenne River, from its mouth to Sheyenne Lake, is 878 km long. (It extends upstream another 36 km as a highly intermittent stream.) Its basin upstream from gaging station 595 (Fig. 1) has an area of about 22973 km² (U.S. Geol. Surv., 1964: 54). The average gradient of the river is 0.28 m/km.

Discharge data for 8 gaging stations are given in Fig. 1. Flow is generally intermittent above station 16, where years in which zero discharge occurs is common. A substantial increase in discharge occurs where the river crosses the Sheyenne delta (from about station 26 to station 29), due primarily to groundwater inflow from the sandy delta deposits (Paulson, 1964). Selected aspects of water chemistry are summarized in Table 1. Specific conductance, pH, chloride, sulfate and bicarbonate content tend to increase downstream, whereas potassium shows no apparent trend for the river.

The bottom sediment generally becomes finer downstream, although it varies considerably in response to the local surficial geology as described above. Turbidity also generally increases downstream as the bottom sediment becomes finer (Cvancara, 1970: 83).

METHODS

Most of the 31 live-mollusk stations (Fig. 1) were established by one of us (RDN) during the summer of 1966, when another of us (AMC) established 5 stations in the lower reaches

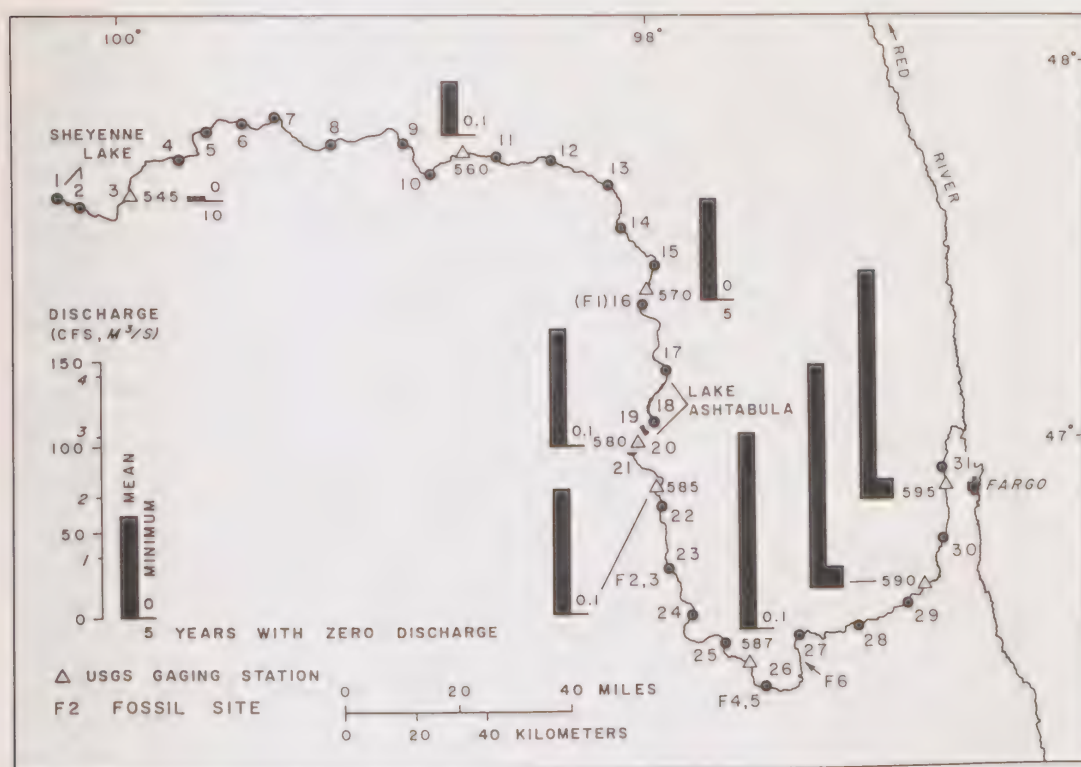


FIG. 1. Location map showing living mollusk stations (solid dots), fossil mollusk sites (F1-F6) and discharge values for 8 USGS gaging stations on the Sheyenne River. Discharge values are for the 10-year span from October 1, 1955 to September 30, 1965 except for gaging station 587; here, the period covered is October 1, 1957 to September 30, 1966. Discharge data were taken from U.S. Geological Survey (1961-1966, 1964). Cfs signifies cubic feet per second.

of the river. In 1968, one of us (AMC) established 2 stations on Sheyenne Lake and, in 1969, 2 stations on Lake Ashtabula. In 1973, 2 of us (AMC and JVA) reoccupied 6 river stations and established another on Lake Ashtabula. In 1974, one of us (AMC) reoccupied 2 additional stations in the lower reaches of the river. Mussels were collected by handpicking by feel with the hands and feet, aided in non-turbid water by a Turtlox Fishscope, an aluminum alloy cylinder (0.61 m long by 0.15 m in diameter) fitted with a glass plate at one end. Other mollusks were usually collected by passing a food strainer (with wire screen) through the bottom sediment and aquatic vegetation. An Ekman dredge and a larger basket dredge were used for a few stations in Sheyenne Lake and Lake Ashtabula.

Fossil mollusks were collected from 6 sites (Fig. 1). About 1- to 2-liter samples were taken from each fossiliferous unit, dry sieved and picked for fossils.

RESULTS

Living mollusks

Thirty-one species were found inhabiting the Sheyenne River: 12 mussels, 6 pill clams and 13 snails (4 prosobranchs and 9 pulmonates) (Table 2). Most species occurred below about station 9. Sixteen species were found in Lake Ashtabula (Fig. 1): 4 mussels, 4 pill clams and 8 snails; 2 of the mussels, *Amblema plicata* and

TABLE 1. Specific conductance and 5 chemical factors for 5 U.S. Geological Survey gaging stations on the Sheyenne River (gaging stations are shown on Fig. 1)^a.

USGS gaging station	Specific conductance (micromhos/cm)	pH	Total chlorides (mg/l)	Total sulfates (mg/l)	Total bicarbonates (mg/l)	Potassium (mg/l)	Time of sampling
560	1760 ^b	8.5	24	264	844	15	Oct. 1, 1955- Sept. 30, 1965
	625	7.7	12	79	294	7.0	
	234	7.1	0.6	28	102	1.9	
570	1080	8.0	26	162	521	11	Oct. 1, 1959- Sept. 30, 1960
	787	7.5	16	124	356	6.7	
	213	6.5	0.1	29	8	6.2	
587	1330	8.3	84	447	459	15	Oct. 1, 1957- Sept. 30, 1965
	782	7.5	34	144	276	11.0	
	295	6.7	8	39	104	5.0	
595	1050	8.0	51	193	344	9.5	Sept. 16, 1969- Sept. 15, 1970
	856	7.6	35	155	305	7.8	
	467	7.4	15	85	172	6.9	
606	1320	8.5	86	260	420	11	July 16, 1969- Sept. 28, 1971
	913	7.9	43	185	303	7.0	
	426	7.1	17	76	143	0.0	

^aData from U.S. Geological Survey 1959-1965; 1970-1973. Locations of gaging stations are shown on Fig. 1.

^bUpper number is the maximum, middle number is the mean, and lower number is the minimum for the interval of time sampled.

Lasmigona complanata, were recovered during a separate SCUBA study (1974) of the lake's mussels to be reported on later and are not listed in Table 1 for the lake. Seven species of mollusks (all snails) were found in Sheyenne Lake. The greatest similarity occurs between assemblages in the river above and below Lake Ashtabula and between assemblages in Lake Ashtabula and in the river above the lake (Table

3). Least similarity occurs between assemblages in Sheyenne Lake and in the river below Lake Ashtabula.

Of the mussels, *Anodonta grandis* and *Lampsilis radiata* occurred most frequently and *Proptera alata* occurred least frequently. Only empty shells were found of *Quadrula quadrula*. Clarke (1973: 33), however, reported it from "1 mi E of Kindred N.D." (near USGS gaging station 590 below station 29; Fig. 1) and said later (letter dated 25 September 1974) that it was collected alive. *A. grandis* was found farthest upstream. Of the 2 species of *Lasmigona*, *L. complanata* occurred at more stations and in greater numbers. For *Lampsilis*, the same was true for *L. radiata*. Mussels occurred on all types of bottom but rarely among cobbles and boulders and in rippled sand.

Of the pill clams, *Pisidium compressum* and *Sphaerium striatinum* occurred most frequently and *S. simile* least frequently. *P. compressum* and *S. lacustre* occurred farthest upstream and *S. transversum* occurred farthest downstream. *P. nitidum* was found in greatest numbers in Lake Ashtabula. In the river, pill clams generally occurred adjacent to the banks where the bottom sediment was finer, usually in muddy very fine to fine sand.

The most frequently found snails were *Physa gyrina* and *Cincinnatia cincinnatiensis* (= *Amnicola integra* (Say)). *P. integra* was found farthest downstream. *Gyraulus circumstriatus* and *Aplexa hypnorum* were found only in Sheyenne Lake. Five snails, *Valvata tricarinata*, *Cincinnatia cincinnatiensis*, *Amnicola limosa*, *Gyraulus parvus* and *Helisoma anceps*, were found generally at greater densities in Lake Ashtabula than elsewhere. *A. limosa* was collected in the river at only one station. Of the 2 species of *Helisoma*, *H. trivolvis* was most frequently observed. In the river, the 4 prosobranch snails (*Valvata tricarinata*, *Probythinella lacustris*, *Cincinnatia cincinnatiensis* and *Amnicola limosa*) occurred in habitats similar to those of the pill clams. Other snails (pulmonates) were found generally crawling on various types of bottom sediment or attached to aquatic vegetation. The limpet *Ferrissia rivularis* was found commonly on mussel shells.

Campeloma decisum was represented only by empty shells at stations 28 and 29 (Fig. 1). Clarke (1973: 218) reported this species from "1 mi E of Kindred" (near USGS gaging station 590 below station 29) and said later (letter dated 25 September 1974) that it was represented by a single empty shell. He also reported (letter cited) empty shells from the Red River at Abercrombie, N. Dak. (Clarke, 1973: 218). In August, 1974, one of us (AMC) collected fossil shells of this species at station 28 from fine to medium sand in a cutbank of the Sheyenne River. It is uncertain whether this species is actually living in the river. Clarke's specimen and a few of ours appear relatively fresh and have a grayish-green periostracum. The nearest live occurrence of this species, of which we are aware, is the Otter Tail River a few kilometers upstream from Fergus Falls, Minnesota, 88.5 air km southeast of station 29. The bottom sediment at station 29 (and station 28) was mostly fine to medium, well-sorted, rippled sand in the main channel and very fine to fine muddy sand along the banks.

Six stations (3, 10, 16, 20, 22 and 29) in September, 1973 and 2 stations (28 and 31) in August, 1974 were recollected to determine if any gross changes in the molluscan fauna had occurred since 1966 when most of the collecting was done. Accounting for differences in season of collecting and different collectors for all stations but 2, no significant changes in the fauna between 1966 and 1973-74 are apparent. The molluscan fauna had apparently not degraded; in fact, additional species were collected at 5 of the 8 stations. The finding of 8 additional mussels at station 31 (Table 2) in 1974 is attributed to much lower river level (and more complete collecting) than was existent in 1966. Most notably, *Ligumia recta* and *Proptera alata* were found living in the river for the first time.

TABLE 2. (Cont.)

	8 (A159)	9 (A148)	10 (A161 A981)	11 (A149)	12 (A142)	13 (A150)	14 (A162)	15 (A163)	16 (A167 A982)	17 (A394)	18 (A166)
Unionacean bivalves											
1.						0.6	1.3	e	e 17.3		
2.						1.1			e 10.6		
3.											
4.	131	4.0	17.3 43.0	13.4	30.0	7.4	42.6	8.0	15.0 22.6		
5.				e	e	18.8	1.3	1.3	e e		
6.	e	e	5.0	8.0	8.0	1.7	6.6		1.0 45.3		
7.				2.7		1.1			1.0		
8.				e		e		e	2.0 1.3		
9.	8.0	50.0	22.6 24.0	e	32.0	25.2	20.0	12.0	22.0 113		
10.											
11.											
12.											
Sphaeriid bivalves											
13.			R							U	
14.	C	A	A		A	A	C	C	A U		
15.			e						R		
16.									e		
17.	R	R	U C	U U						C C	
18.											
Gastropods											
19.											
20.			A e	U						A	C
21.	X		X C		C				C	U	A
22.			X		e						
23.			X e							U	C
24.											
25.				X							
26.											
27.		U	U C						A		
28.											
29.										C	
30.										e	
31.											C
32.		R		R						U	
33.			e			U				U	
34.		C	C	A		U				A	
35.											
36.											R
Predom- inant bottom sediment	GS	GS	GSM MS	S	GS	SG	SG	S	GS GS	GS	GS

TABLE 2. (Cont.)

	29 (A110 A986)	30 (A111)	31 (A108 A1062)	
Unionacean bivalves				
1.	0.8		U	
2.	0.8		U	
3.			e	
4.	1.7	3.0	A	
5.				
6.	3.6		A	
7.	1.7			
8.			R	
9.	1.2		U	
10.	1.2	3.0	U	
11.			R	
12.			R	
Sphaeriid bivalves				
13.				
14.				
15.	e		e	
16.	U		C	
17.				
18.				
Gastropods				
19.	e			
20.				
21.	e		e	
22.			e	
23.	e			
24.	U			
25.	e			
26.				
27.				
28.				
29.				
30.				
31.				
32.	e			
33.				
34.				
35.				
36.	e		R	e
Predominant bottom sediment	S	MS	MS	M

^a Accession numbers of the University of North Dakota, Department of Geology.

^b Numerical values are the individuals of unionacean bivalves collected per hour by 2 collectors. Letters for estimated relative abundance are: A=abundant, C=common, U=uncommon, and R=rare; X=present but relative abundance unknown and e=empty shells.

cSG=sandy gravel, MSG=muddy sandy gravel, GS=gravelly sand, S=sand, MS=sandy sand, SGH=sandy gravelly mud, GSM=gravelly sandy mud, SM=sandy mud, and M=mud, which is mixture of silt and clay.

TABLE 3. Jaccard's similarity coefficients^a comparing numbers of molluscan species by group and general location.

	Sheyenne Lake	Above Lake Ashtabula	Lake Ashtabula	Below Lake Ashtabula
Above Lake Ashtabula	M 00 ^b P 00 S 36 A 18			
Lake Ashtabula	M 00 P 00 S 25 A 15	M 50 P 67 S 67 A 62		
Below Lake Ashtabula	M 00 P 00 S 14 A 07	M 73 P 50 S 62 A 63	M 36 P 17 S 54 A 39	
Fossils	M 00 P 00 S 25 A 12	M 64 P 33 S 67 A 59	M 40 P 20 S 45 A 38	M 75 P 67 S 54 A 65

^aCheetham & Hazel (1969).

^bM=mussels; P=pill clams; S=snails; A=all mollusks; zero values reflect that no mussels or pill clams were found in Sheyenne Lake.

Fossil mollusks

Fossil mollusks were discovered at 6 sites at the middle and lower-middle reaches of the river (Fig. 1). At sites F1-F5, fossils were collected from cut-bank exposures 0.6-3.0 m above river level. At F6, fossils were taken from a road-cut exposure about 11 m above river level. Most of the fossils occurred in sandy mud and muddy sand.

Twenty species of aquatic mollusks were found as fossils at the 6 sites: 10 mussels, 2 pill clams and 8 snails (Table 4). In addition, the snail *Campeloma decisum* was found (1974) as a fossil at station 28. Shells of the snail *Cincinnatia cincinnatiensis* and pill clam *Sphaerium striatinum* were most numerous as fossils. Shells of mussels were generally sparse. Land snails occurred in about one-half of the samples.

DISCUSSION

Living mollusks and ecologic factors

Perhaps the primary ecologic factor influencing the occurrence of mollusks in the Sheyenne River is river discharge. Low discharge or high frequency of zero discharge appears to correlate with low diversity of mussel species in the upper reaches of the river (Fig. 1, Table 2); high discharge appears to correlate with

TABLE 4. Occurrence and relative abundance of fossil mollusks at 6 sites on the Shenoye River (Fig. 1 shows location of fossil sites and Table 2 explains symbols).

Mollusk species	Fossil site and fossiliferous unit					
	F1 Unit 2 (A189) Unit 4 (A188) Unit 8 (A187)	F2 Unit 2 (A186)	F3 Unit 2 (A180) Unit 4 (A179) Unit 6 (A178) Unit 8 (A177)	F4 Unit 2 (A185) Unit 3 (A184)	F5 Unit 2 (A183) Unit 3 (A182)	F6 Unit 2 (A181)
Unionacean bivalves						
1. <i>Ambleria plicata</i> (Say)				U	R	
2. <i>Fusconaia flava</i> (Rafinesque)				R	U	
3. <i>Quadrula quadrula</i> (Rafinesque)				R	R	
4. <i>Anodonta grandis</i> Say	R		R	U		
5. <i>Anodontoides ferussacianus</i> (Lea)	R					
6. <i>Lasmigona complanata</i> (Barnes)	R	R		R		
7. <i>Strophitus undulatus</i> (Say)	R		R	U		
8. <i>Lampsilis ovata</i> (Say)	R			U		
9. <i>L. radiata</i> (Gmelin)	U			U		
10. <i>Ligumia recta</i> (Lamarck)						C
Sphaeriid bivalves						
11. <i>Sphaerium striatinum</i> (Lamarck)	A		C	A	C	C
12. <i>Pisidium compressum</i> Prime	R			U	U	
Gastropods						
13. <i>Cincinnatia cincinnatiensis</i> (Anthony)	C					
14. <i>Probythinella lacustris</i> (Baker)	A		U	A	A	
15. <i>Stagnicola caperata</i> (Say)	R		R	C	A	
16. <i>Ferrissia rivularis</i> (Say)			R			R
17. <i>Gyraulus parvus</i> (Say)	R					
18. <i>Helisoma anceps</i> (Menke)				U	U	
19. <i>H. trivolvis</i> (Say)	R			R	R	
20. <i>Physa integra</i> Say				R	R	
Predominant sediment type	SM	MS	SM SM SM	MSG MS	S CS	S
Thickness of unit (m)	0.18 0.18 0.18	0.61	0.24 0.12 0.09 0.09	0.24 0.67	0.24 0.30	1.0

^a Accession number of University of North Dakota, Department of Geology. Units with lower unit numbers are relatively older.

high mussel diversity downstream. Low or zero discharge may be detrimental because of lowered dissolved oxygen, higher concentrations of dissolved salts, and increased predation accompanying the lowering of river level (Cvancara, 1970: 87).

The relationship of discharge to the other mollusks seems to be more complex. Certain pill clams and snails occurred more frequently in stagnant (non-flowing)

water and others in flowing water. In this connection, the possible impact of Lake Ashtabula on the Sheyenne River molluscan fauna is instructive. Under Results, we stated that 1 pill clam and 5 snails generally occurred in greater numbers in the lake than elsewhere. Mussel diversity was also low in the lake (unpubl. results of 1974 study with SCUBA); *Anodonta grandis*, generally in greatest numbers in stagnant or slow-moving parts of the river, was the dominant mussel in the lake. Sheyenne Lake was characterized by certain stagnant-water species, 2 of which differed from those in Lake Ashtabula. On the other hand, species such as the pill clam *Sphaerium striatinum* and the snail *Ferrissia rivularis* seem to prefer flowing water and neither was found in Lake Ashtabula nor Sheyenne Lake.

An unstable bottom, such as one of rippled sand, seems to be a primary factor in restricting mollusks of all types. This condition was generally found where the river crosses the Sheyenne delta, and mollusks were generally sparse at stations 26-29 (Fig. 1, Table 2).

Perhaps high turbidity is a limiting factor in the lower reaches, for pill clam and snail diversity tended to decrease (Table 2) as turbidity increased markedly (Cvancara, 1970: fig. 9).

Imlay (1973) demonstrated that dissolved potassium at low levels is toxic to mussels and presented a predictive hypothesis: rivers with 4 mg/l K would contain mussels, those with 7 mg/l K (or greater) would have no mussels, and those with 4-7 mg/l K would be marginal for mussels. (Three of the 4 species he experimented with, *Amblema plicata*, *Fusconaia flava* and *Lampsilis radiata*, also inhabit the Sheyenne River.) At 5 gaging stations the mean potassium concentration was 6.7-11 mg/l with a maximum of 15 (Table 1) at 2 stations. Below gaging station 587 (Fig. 1), with a mean potassium concentration of 11 mg/l, mussel density appeared to be less than in the river directly above; mussel diversity, however, remained high at 10 species. Imlay (1973: 108) admitted that the (lower) Sheyenne River "slightly erodes the predictive hypothesis."

One of us has suggested (Cvancara, 1970: 87) that high chloride content may restrict the occurrence of mussels in 3 Red River tributaries of eastern North Dakota, and other mollusks may also be so affected (Cvancara, Erickson & Delimata, 1972). Imlay (1973: 108) pointed out that in the lower reaches of one of these tributaries (Park River) where the chloride content was high and mussels were absent, the potassium content was also high. He also cited some evidence (p 109) that the chloride ion is less toxic than the potassium ion. High chloride values (up to 86 mg/l) do not necessarily correspond to high potassium values in the Sheyenne River (Table 1). Further work in natural habitats is necessary to evaluate the relative effects of potassium and chlorides on mollusk occurrences.

Availability of suitable fish host may affect the occurrence of mussels in the Sheyenne River. The fish fauna is more diversified below the dam that forms Lake Ashtabula than above it, and fishes of the lower Sheyenne have been prevented from migrating into the upper reaches by the dam (Tubb, Copes & Johnston, 1966: 125). (Fish populations above the dam have resulted from planned or indiscriminate stocking.) Likewise, the mussel fauna is more diversified below the dam than above it. Two mussels, *Lampsilis ovata* and *Ligumia recta*, were found alive only below Lake Ashtabula; their distribution may be related to restricted occurrence of fish hosts. The known natural fish hosts of *L. ovata* are white crappie (*Pomoxis annularis*) and sauger (*Stizostedion canadense*), and those of *L. recta* are white crappie and bluegill (*Lepomis macrochirus*) (Coker et al., 1921: 153). These 3 fishes have been reported only from Lake Ashtabula or below it and not above it (Tubb, Copes & Johnston, 1966). The bluegill has been introduced into the lake (Farmer, 1974: 6).

Comparison of fossil and living faunas

The fossil molluscan fauna generally resembled the living fauna but lacked 13 species. Two mussels, 4 pill clams and 7 snails were not found as fossils. No fossil species were different from those living now, with the possible exception of the snail *Campeloma decisum* whose existence in the Sheyenne is uncertain. The predominance of mostly smaller fossil mollusks is possibly partly the result of destruction of thinner-shelled forms and selective sorting of smaller forms during transportation. Two apparent anomalies are the presumed lack of *Valvata tricarinata* and the presumed more frequent occurrence of *Probythinella lacustris* in the fossil material.

The total fossil fauna is most similar to those assemblages below Lake Ashtabula except for the snails (Table 3). This might be expected as most of the fossil sites are below the lake. Least similarity occurs between the fossil fauna and that found living in Sheyenne Lake.

Age of fossil mollusks

Limited age information is available for the fossil mollusks. At site F6 (Fig. 1, Table 4), shells of the mussel *Lampsilis radiata* from a fluvial terrace about 11 m above the river have been dated at $13,500 \pm 220$ years before present (I-2289; Moran et al., 1973: fig. 2 and p 42). Between stations 27 and 28 (Fig. 1), "clam shells" from fluvial sediment of the "ancestral" Sheyenne have been dated at $12,000 \pm 250$ years before present (I-2537; Moran et al., 1973: 11). Just below station 28, or about 56 river kilometers below site F6, *Lampsilis radiata*, at least 2 pill clams and 4 aquatic snails were recovered from silty clay just above river level (Tuthill, 1964). These mollusks were directly associated with wood dated at $2,540 \pm 300$ years before present and were considered to have been deposited by the "modern" Sheyenne River (W-1185; Moran et al., 1973: 28). Therefore, mollusks inhabited the "ancestral" Sheyenne River that flowed into glacial Lake Agassiz at least as early as about 13,500 years ago and the "modern" Sheyenne at least as early as about 2,500 years ago. Fossil mollusks from sites F1-F5 probably date within this time interval (2,500 - 13,500 years) or are younger.

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A SUMMARY OF PULMONATE DISTRIBUTION INFORMATION
CONTAINED IN ZILCH'S 1959-1960 MONOGRAPH:
GASTROPODA, TEIL 2, EUTHYNEURA¹

George A. Te

ABSTRACT

The mass of information on the distribution of pulmonate snails at the sub-generic level contained in Zilch's monograph (1959-1960) was processed by computer. Distribution ranges and patterns, which are essentially a summary and a quantification of that treatise, were generated.

This paper presents the following: (1) A guide map; (2) A verbal summary of distribution ranges and other distributional information for each pulmonate family; (3) A numerical account of the distribution of each pulmonate family; and (4) A list of patterns of distribution.

This paper is intended to be only a summary of a basic taxonomic reference book (Zilch's monograph) with respect to distributional information. Any zoogeographic interpretation from the summaries should consider both the accuracy of the data source and subsequent changes in taxonomy and distribution records.

INTRODUCTION

This work is a summary of the raw distribution information contained in Zilch's monograph (1959-1960). The distributional data were taken directly from the monograph, with no further updating. It should be understood then that this is a static summation of a basic reference source and not a zoogeographic study. Any zoogeographic interpretation from the summaries should take into consideration the accuracy of the distributional information and the subsequent changes in taxonomy and additional distribution records since the publication of Zilch's monograph. Although the format adapted here oversimplifies the complexity of actual distributions in many respects, it is hoped that critical readers will appreciate the heuristic value of the present study.

Presented are:

1. A guide map with coded areas and their corresponding area descriptions with detailed notes (Fig. 1 and Table 1).
2. A Verbal summary of the distributional ranges for each pulmonate family with related information (p 40, 44-48).
3. A numerical account of pulmonate family distributions in terms of number of genera and subgenera found in each area of the world (p 48, 53 and Table 2).
4. A list of patterns of distribution found in the pulmonates at the family level (Table 3 and p 53).

MATERIALS AND METHODS

The system of classification adopted in this study is that of Taylor & Sohl (1962). The

¹In: Schindewolf, *Handbuch der Palaeozoologie*, Vol. 6. Borntraeger, Berlin. Lief. 1-4, 6: 834 p.

distribution information was taken from Zilch (1959-1960). The base map used was Stieler's (1926-1928) Hand-Atlas, 10th ed. The climatic zones considered follow those outlined in the World Maps of Climatology by Landsberg *et al.* (1966). The data were processed through the MTS (Michigan Terminal System) computer. Distribution ranges of pulmonate families and family subgroups were generated by computer from subgenus and up. Only family distribution ranges are reported in the present paper.

The basic taxonomic unit used is the subgenus. In place of taxonomic names, nomenclature was used to facilitate computer processing. Distribution information was translated and coded into 39 map units (= areas). These units were arrived at by superimposing a climatic map on Wallace's (1876) 24 zoogeographical subregions (see Fig. 1 and Table 1). Only taxa with Recent representatives were included, and only their Recent distribution ranges. Subgenera preceded with question marks (?) in Zilch's monograph were excluded from the study. Other information provided here, such as climatic zone distribution and mainland vs. island forms and inland freshwater vs. coastal marine or brackish water forms, were taken from related unpublished studies done by the author.

Anyone wishing more information on the nomenclature used, the coding system adopted, or additional details of family subgroup distribution (e.g., at the subfamily, tribal or generic levels) should contact the author.

DISTRIBUTION RANGES OF PULMONATE FAMILIES

Verbal summaries of distribution ranges and related distribution information for each family are presented below. The distribution of the 13 basommatophoran families are presented first, followed by those of the 63 stylommatophoran families. The order of presentation is by distribution patterns, which is essentially an improved version of a system devised earlier by the author (Te, 1972). A listing of this revised version of pulmonate distribution patterns is provided in Table 3.

Included in each family caption are the following entries:

1. Total number of genera and subgenera. This is the number in parentheses following the family name. This number is an indicator of the relative size of the family. The figure given is a total figure which includes fossil forms and those with questionable taxonomic status, both of which have been excluded from computer processing.
2. Climatic zone distribution. Climatic zones considered in this study are: tropical, warm-temperate subtropical, cool-temperate, cold-temperate boreal, polar and subpolar. These are shortened to tropical, subtropical, temperate, boreal and subpolar, respectively, as used in the entries.
3. Statement on habitat. A statement is provided as to whether the family is inland-freshwater or coastal-marine or brackish water in the case of Basommatophora, and mainland or island forms in the case of Stylommatophora.
4. Verbal account of the distribution ranges. For details on the geographic terminology used, see the footnotes to Table 1.
5. Statement of endemism (if applicable). The term "endemic" as used here refers to families confined to one region, e.g., Africa, or Western Palaearctic. Families with distributions much smaller than a region are considered highly endemic.
6. Statement on diversity. This refers only to subgeneric diversity and does not measure diversity at the species level. Diversity progression is from no statement, which means low diversity, to more diversity, to relatively diversified, to relatively high diversity, to high diversity, and finally to very high diversity.
7. Possible alternate pattern (if applicable). Where family distribution can be grouped under a pattern other than the one designated for it, a statement is inserted

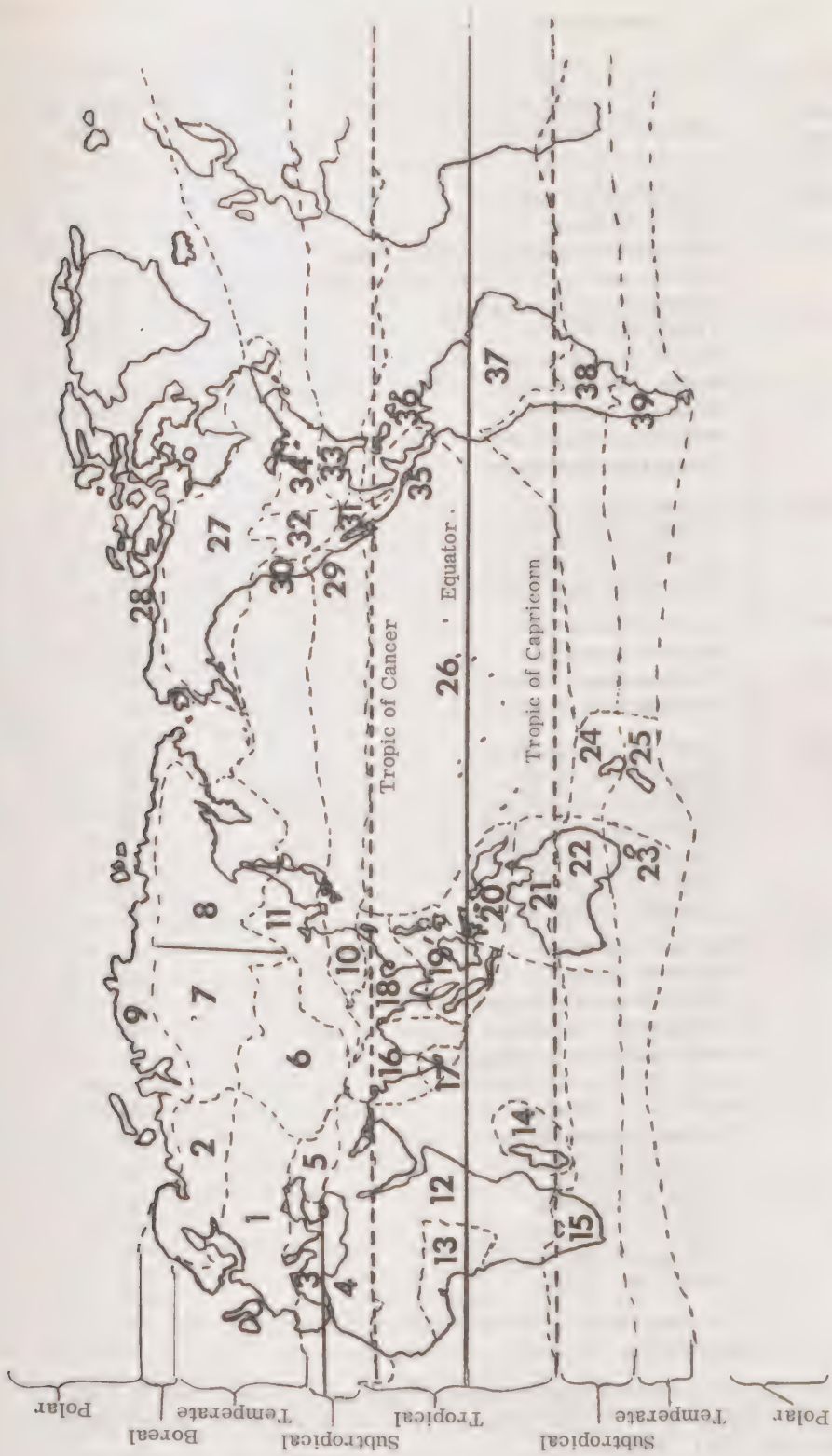


FIG. 1. Guide map with the land masses of the world divided into 39 coded areas. Descriptions of each of the 39 areas are provided in Table 1 and in subsequent notes. The purpose of this map is to add precision to geographical terms used in the text and tables and to assist readers who may wish to plot distributional information contained in Table 2.

TABLE 1. Description of the 39 areas on the guide map.

Wallace's regions ¹	Area descriptions ² (Wallace's subregions + climatic divisions)	Area codes on guide map
Palearctic	Temperate European	1
	Boreal European	2
	Subtropical European-Mediterranean ³	3
	Subtropical North African-Mediterranean	4
	Temperate Mediterranean	5
	Temperate Siberian	6
	Boreal West-Siberian ⁴	7
	Boreal East-Siberian	8
	Subpolar Siberian	9
	Subtropical Manchurian	10
	Temperate Manchurian	11
Ethiopian	Tropical East Africa	12
	Tropical West Africa	13
	Tropical Malagasy ⁵	14
	Subtropical South Africa	15
Oriental	Tropical Indian	16
	Tropical Ceylonese	17
	Tropical Indo-Chinese	18
	Tropical Indo-Malayan	19
Australian	Tropical Austro-Malayan	20
	Tropical Australian	21
	Subtropical Australian	22
	Temperate Australian ⁶	23
	Subtropical New Zealand	24
	Temperate New Zealand	25
	Tropical Polynesian ⁷	26
Nearctic	Boreal Canadian	27
	Subpolar Canadian	28
	Subtropical Californian	29
	Temperate Californian	30
	Subtropical Rocky Mountain	31
	Temperate Rocky Mountain	32
	Subtropical Alleghany	33
	Temperate Alleghany	34
Neotropical	Tropical Mexico	35
	Tropical Antillean	36
	Tropical Brazilian	37
	Subtropical Chilean	38
	Temperate Chilean	39

¹ Alfred R. Wallace (1876).² 39 areas were arrived at by superimposing Wallace's 24 subregions on a climatic map. This gives a total of 37 areas; 2 of the 37 areas were further split; see footnotes 3 and 4 below.

TABLE 1. (Cont.)

³Subtropical Mediterranean was split into European and North African Mediterranean areas. The very high diversity along the European coast of the Mediterranean necessitated this split to increase resolution.

⁴The Boreal Siberian area was split into western and eastern sectors. The vastness of the Boreal Siberian area necessitated differentiation of the coastal sector from the interior sector. This was done to increase resolution.

⁵Malagasy includes Madagascar and the outlying island groups such as Mauritius, Reunion and Seychelles.

⁶Temperate Australia includes the temperate part of continental Australia and Tasmania.

⁷Tropical Polynesia includes the Micronesian, Melanesian and Polynesian island groups.

Notes to Table 1 on various other geographic terminologies used:

1. Orient as a regional term includes India, Ceylon, Indo-China, southern China and the Indo-Malayan islands of Sumatra, Java, Borneo and the Philippines.

2. South Asia includes the tropical Indian and tropical Ceylonese areas.

3. Southeast Asia includes the tropical Indo-China and tropical Indo-Malayan areas.

4. East Asia encompasses the subtropical and temperate Manchurian Palaearctic plus the Indo-China and Indo-Malayan areas.

5. Western Palaearctic as a regional term encompasses the European and Mediterranean subregions of Wallace. It is bounded on the east by the Ural Mountains, the Caspian Sea and the eastern reaches of the Plateau of Iran.

6. Manchurian Palaearctic as a regional term includes China north of Yunan Plateau and Nan Ling Mountain, excluding the western highlands and Inner Mongolia. It also includes Korea, Japan and a narrow strip extending around the high slopes of the Himalayas.

7. Siberian Palaearctic as a regional term includes Turkestan, the whole of Siberia, Mongolia, Inner Mongolia and the western highlands of China (Sinkiang, Kansu, Tsinghai and Tibet).

8. North America as a regional term is used equivalent to Nearctic; it includes Greenland, Bermuda islands and continental North America down to the subtropical part of Mexico.

9. Middle America as a regional term ranges from Mexico to Panama; it includes southern Florida, the southern tip of Texas, Baja California, the tropical part of Mexico, the West Indies and the whole of mainland Central America.

10. West Indies corresponds to the tropical Antillean area as outlined on the Guide Map.

11. South America as a regional term ranges from southern Panama down through the whole of continental South America. It also includes the island groups of the Galápagos and Juan Fernández on the Pacific side and Fernando de Noronha on the Atlantic side.

12. Australia used as a regional term includes continental Australia, Tasmania and the Austro-Malayan islands of Celebes, Moluccas and New Guinea.

13. Pacific used as a regional term includes the island groups of Micronesia, Melanesia, Polynesia and New Zealand.

14. Africa used as a regional term is equivalent to Wallace's Ethiopian region; it encompasses tropical Arabia and all of Africa below the Tropic of Cancer, as well as the island groups of Madagascar, Mauritius and Seychelles.

15. Tropical Africa includes the tropical West African and tropical East African areas.

16. Holarctic refers to the distribution range which encompasses the composite northern land masses of North America and the Palaearctic regions.

17. Pantropical refers to the distribution range which covers the regions circumscribed by the tropical belt around the world. It extends from the tropical to subtropical parts of the world and usually includes Africa, the Orient, the Pacific, Middle America and parts of Australia and South America.

18. Southern hemisphere refers to areas south of the equator.

to that effect, following the word "Possible".

8. Fossil information (if applicable). Fossil information is provided and indicated in parenthesis only when considered important, such as when fossil records show a different distribution range from that of the Recent representatives of the family. However, fossil information does not figure into the distribution range (which is concerned only with the Recent fauna).

A. BASOMMATOPHORA

- I. *World-wide and nearly world-wide*: Includes 7 families. Distribution covers all zoogeographic regions (excluding Antarctica).

a) Inland:

1. Planorbidae (84 genera and subgenera). Tropical to boreal; primarily inland-freshwater. World-wide. High diversity in all regions except southern Australia and Pacific regions.
2. Lymnaeidae (34). Tropical to boreal; primarily inland-freshwater. World-wide. More diversity in North America; sparse in southern hemisphere.
3. Physidae (6). Tropical to boreal; primarily inland-freshwater. World-wide. More diversity in North America; moderate in northern Palaearctic and Middle America; sparse elsewhere.
4. Ancyliidae (15). Tropical to boreal; primarily inland-freshwater. Nearly world-wide; absent in northern part of Siberian and Manchurian Palaearctic. More diversity in North America, South America and Africa.

b) Coastal:

5. Ellobiidae (55). Tropical to temperate; primarily coastal-marine or brackish water. World-wide; absent in western Siberian Palaearctic. High diversity in East Indies and tropical Pacific islands; moderate in Mediterranean areas, Africa and Middle America; sparse elsewhere.
6. Siphonariidae (19). Tropical to temperate; primarily coastal-marine or brackish water. Nearly world-wide; absent in northern Palaearctic and eastern North America. More diversity in Australia.
7. Trimusculidae (Gadiniidae) (1). Tropical to temperate; primarily coastal-marine or brackish water. Nearly world-wide; present in coastal Mediterranean areas, West and South Africa, Malagasy, Indo-Malayan, Australian regions and Pacific coast of the Americas.

- II. *Endemic and semi-endemic*: Includes 6 families. Distribution restricted to 1 zoogeographic region. Those with greater than 1 zoogeographic region are considered semi-endemic.

a) Inland:

1. Lancidae (4). Subtropical to boreal; primarily inland-freshwater. Endemic; restricted to North America.
2. Acroloxidae (3). Subtropical to boreal; primarily inland-freshwater. Semi-endemic; found in Europe and Lake Baikal (Siberia). (Paleocene fossil in North America.)
3. Chilinidae (1). Tropical to temperate; primarily inland-freshwater. Highly endemic; restricted to southern South America.
4. Latiidae (1). Subtropical to temperate; primarily inland-freshwater. Highly endemic; found only in New Zealand.

b) Coastal:

5. Amphibolidae (2). Tropical to temperate; primarily coastal-marine or brackish water. Semi-endemic; found in East Asia, Australia and Pacific regions.
6. Otinidae (2). Temperate; primarily marine-coastal water. Highly endemic; restricted to coast of southwestern British Isles and northern France. (Possible Jurassic fossil in North America.)

B. STYLOMMATOPHORA

- I. *World-wide*: Includes 8 families, 2 of which belong to a subpattern. Distribution covers all zoogeographic regions (excluding Antarctica).

1. Endodontidae (106 genera and subgenera). Tropical to temperate (extending to boreal); more island forms. World-wide. Highest diversity in the New Zealand area; high diversity in South African, Australian, Polynesian and North American regions.
2. Euconulidae (94). Tropical (extending to boreal); primarily island form. World-wide. Very high diversity in the Pacific islands; relatively high diversity in Indo-Malayan and Austro-Malayan island groups and in Middle America.
3. Vertiginidae (39). Tropical to subtropical (extending to boreal); more island forms. World-wide. More diversity in Hawaii; sparse in the southern hemisphere; moderate elsewhere.

4. Chondrinidae (34). Tropical to temperate (extending to boreal); primarily mainland. World-wide. More diversity in the southern Europe-Mediterranean area, Southeast Asia and South China.
5. Pupillidae (27). Tropical to boreal; more mainland forms. World-wide. More diversity in Western Palaearctic.
6. Succineidae (26). Tropical to boreal; primarily mainland. World-wide. More diversity in Western Palaearctic and North America.

a) *Nearly world-wide:*

7. Clausiliidae (227). Tropical to temperate; primarily mainland. Nearly world-wide; absent in Australia, North America and Siberian Palaearctic. Very high diversity in southern Europe-Mediterranean area; generally high diversity in the rest of Western Palaearctic, South China, Indo-China and South America; sparse elsewhere.
8. Valloniidae (19). Tropical to boreal; more mainland forms. Nearly world-wide. More diversity in North America and Western Palaearctic; sparse or absent in parts of southern hemisphere.

II. *Pantropical:* Includes 3 families, 1 of which belongs to a subpattern. Distribution covers all regions within the tropical belt. Includes Africa, Orient, Pacific, Middle America and parts of Australia and South America.

1. Streptaxidae (87). Tropical (extending to subtropics); primarily mainland. Pantropical; absent in tropical Australia, Pacific and Middle American regions. High diversity in tropical Africa. (Cretaceous to Eocene fossil in Europe.)
2. Subulinidae (80). Tropical to subtropical; primarily mainland. Pantropical. High diversity in tropical Africa and tropical South America. (Paleocene fossil in North America.)

a) *Extended to Western Palaearctic:*

3. Ferrussaciidae (20). (see VIIIb.)

III. *Holarctic:* Includes 5 families, 2 of which belong to a subpattern. Distribution encompasses all northern land masses from North America to the Palaearctic.

1. Zonitidae (93). Subtropical to temperate (extending to tropics and boreal); primarily mainland. Holarctic; extending to Middle America and Hawaii. High diversity in Western Palaearctic and North America.
2. Vitrinidae (14). Subtropical to boreal; primarily mainland. Holarctic. More diversity in Western Palaearctic.
3. Cionellidae (Cochlicopidae) (14). Subtropical to boreal (extending to tropics); more mainland forms. Holarctic. More diversity in Western Palaearctic.

a) *Nearly Holarctic:*

4. Arionidae (24). Subtropical to temperate; primarily mainland. Nearly Holarctic; found in Mediterranean region, Manchurian Palaearctic and western North America; extends to upper part of Middle America and also present in South Africa. More diversity in western North America and Western Palaearctic.
5. Limacidae (26). (see VIIIc.)

IV. *South and East Asia, Australian-Pacific, Middle and South America:* Includes 1 family. Not present in Africa, Palaearctic and North America.

1. Camaenidae (Pleurodontidae) (94). Tropical (extending to subtropics and temperate); primarily island form. Distribution includes South Asia, East Asia, New Guinea, Australia, Melanesian islands, Middle America and South America. Highly diversified in Orient, New Guinea and West Indies.

V. *East Asia-America:* Includes 1 family. Distribution includes Manchurian Palaearctic, parts of Orient and the 3 Americas.

1. Philomycidae (1). Tropical to temperate; equally distributed on island and mainland. Distribution includes Indo-China, Indo-Malayan islands, Japan, Formosa and North, Middle and South America.

VI. *Africa-Orient-Palaearctic:* Includes 1 family. Distribution covers the whole of the Old-World.

1. Emidae (80). Tropical to temperate (extending to boreal); primarily mainland. Old-World distribution. High diversity in the Mediterranean region; relatively high diversity in the Manchurian Palaearctic and Indo-Chinese regions.

VII. *Palaearctic:* Includes 2 families. Distribution encompasses 3 regions: Western Palaearctic, Siberian Palaearctic and Manchurian Palaearctic.

1. Pyramidulidae (1). Subtropical to temperate; equally distributed on mainland and island.

Palaeartic; absent in northern Palaeartic.

2. Helicidae (192). (see VIIa.)

VIII. *Western Palaeartic*: Includes 9 families, 3 of which belong to subpatterns. A highly endemic region. Distribution corresponds exactly to Wallace's European and Mediterranean subregions.

1. Trigonochlamydidae (7). Subtropical to temperate; mainland form. Highly endemic; restricted to Caucasus-Persian region.
2. Orculidae (5). Subtropical to temperate; mainland forms. Endemic; restricted to southern Europe and Mediterranean areas.
3. Parmacellidae (5). Subtropical to temperate; primarily mainland. Endemic; restricted to Western Palaeartic.
4. Milacidae (4). Subtropical to temperate; mainland forms. Endemic; restricted to southern Europe and Mediterranean areas.
5. Testacellidae (3). Subtropical to temperate; more island forms. Endemic to southwestern Europe and North Africa.
6. Pleurodiscidae (1). Subtropical; equally distributed on mainland and islands. Endemic to south Italy, some Mediterranean islands, southern and eastern Mediterranean regions.

a) *Extended to Siberian Palaeartic*:

7. Helicidae (192). Subtropical to temperate; primarily mainland. Mainly Western Palaeartic; extend to Siberian Palaeartic; absent in Manchurian Palaeartic. Very high diversity in Western Palaeartic. Possible: Palaeartic pattern.

b) *Extended to the tropics*:

8. Ferrussaciidae (20). Tropical to subtropical; primarily mainland. Western Palaeartic; extend to Africa, India, East Indies, Middle America and Hawaii. More diversity in Mediterranean region. Possible: Pantropical extended to Western Palaeartic subpattern. (Fossil record in Europe dating back to Eocene.)

c) *Extended to North America*:

9. Limacidae (26). Subtropical to temperate (extending to boreal); primarily mainland. High diversity in Western Palaeartic, especially in the Mediterranean area; 1 genus in North America. Possible: nearly Holarctic subpattern.

IX. *Africa*: Includes 6 families, all endemic to Africa. Distribution corresponds to Wallace's Ethiopian region.

1. Urocyclidae (44). Tropical (extending to subtropics); primarily mainland. Endemic to Africa. High diversity in tropical Africa.
2. Achatinidae (23). Tropical (extending to subtropics); primarily mainland. Endemic to Africa. Relatively high diversity in tropical Africa.
3. Dorcasiidae (3). Subtropical; mainland forms. Highly endemic; restricted to South and Southwest Africa.
4. Aillyidae (1). Tropical; mainland forms. Highly endemic; restricted to Cameroons (West Africa).
5. Chlamydephoridae (1). Subtropical; mainland forms. Highly endemic; restricted to South Africa.
6. ?Thyrophorellidae (1). Tropical; found only on an island. Highly endemic; restricted to the island of São Tomé (Gulf of Guinea, West Africa).

X. *East Asia-Africa*: Includes 4 families, 2 of which belong to a subpattern. Distribution includes Africa, Orient and Manchurian Palaeartic; in most cases extends to parts of Siberian Palaeartic.

1. Bradybaenidae (Eulotidae, Fruticicolidae) (80). Tropical to temperate; equally distributed on mainland and islands. Distribution includes tropical Africa, East Asia and southwestern Siberian Palaeartic; 1 group found in Western Palaeartic; absent in India. High diversity in East Asia. (Paleocene fossil in Europe.)
2. Corillidae (8). Tropical to subtropical (extending to temperate); primarily mainland. Distribution includes West and South Africa, southern India, Indo-China; extend to Manchurian Palaeartic. More diversity in Indo-China.

a) *Extended to Australian-Pacific*:

3. Ariophantidae (73). Tropical (extending to subtropics and temperate regions); equally distributed on mainland and islands. Distribution includes East and Southeast Africa, Madagascar and the whole of the Orient; present in New Guinea; extends northward to Manchurian Palaeartic and southwestern Siberian Palaeartic; 1 group in southern Australia and Tasmania. Highly diversified in Orient.
4. Helicarionidae (69). Tropical (extending to subtropics and temperate); primarily island form. Distribution extends from Orient to Pacific; present in Australia, Madagascar and Mauritius-

Reunion island groups; 1 genus in San Thomé (=São Tomé, Gulf of Guinea, West Africa); a few groups extend to Manchurian Palaearctic. Relatively high diversity in the Orient and Malagasy regions.

XI. North, Middle and South America: Includes 1 family. Distribution encompasses all 3 Americas.

1. Helminthoglyptidae (51). Tropical to subtropical (extending to temperate regions); primarily mainland. Distribution includes all 3 Americas; absent in eastern North America, except Florida. Relatively high diversity in southwestern North America and Middle America.

XII. North America: Includes 5 families, 1 of which belongs to a subpattern. Distribution ranges through North America and usually extends to parts of Middle America.

1. Polygyridae (34). Tropical to boreal; primarily mainland. North America; extend to Middle America, especially Mexico and West Indies. High diversity in North America.
2. Haplotrematidae (8). Tropical to temperate; primarily mainland. Distributed in western and eastern coastal states of North America; present in West Indies and Venezuela.
3. ? Ammonitellidae (5). Subtropical to temperate; mainland forms. Found mostly in western North America.
4. Oreohelicidae (2). Subtropical to temperate; mainland forms. Endemic to western North America. (Cretaceous and Paleocene fossil in eastern North America.)

a) *Extended to Middle America:*

5. ? Thysanophoridae (10). (see XIIIa.)

XIII. Middle America: Includes 7 families, 3 of which belong to subpatterns. Distribution range usually includes Middle America, southern North America and northern South America.

1. Urocoptidae (Cylindrellidae, Eucalodiidae) (79). Tropical to subtropical; primarily island forms. Endemic to Middle America; extends slightly to southern North America and northern South America. High diversity in Middle America, especially in the West Indies.
2. Sagdidae (21). Tropical (extending to subtropics); primarily island forms. Endemic to Middle America; present in Florida, Bermuda, Venezuela; absent in mainland Central America. Relatively high diversity in West Indies.
3. Oleacinidae (12). Tropical; primarily island forms. Highly endemic; present only in West Indies and south Florida. Relatively diversified in West Indies.
4. Ceriidae (Cerionidae) (5). Tropical; primarily island forms. Highly endemic; restricted to West Indies. (Miocene fossil in Florida; Pleistocene fossil in Venezuela.)

a) *Extended to North America:*

5. ? Thysanophoridae (10). Tropical to subtropical (extending to temperate); primarily mainland. Distribution includes Middle America; extends to North America and Colombia (northeastern South America). More diversity in Middle America and southern North America. Possible: North America extended to Middle America subpattern. (Fossil records in North America dating back to Paleocene.)

b) *Extended to Mediterranean:*

6. Spiraxidae (44). Tropical to subtropical; primarily mainland. Middle American; extend to southern North America and northern South America; present in northeastern Mediterranean region and in Algeria. High diversity in Middle America. (Fossil records in Europe dating back to Paleocene.)

c) *Extended to South Africa:*

7. Amphibulimidae (8). Tropical to subtropical; more island forms. Present in tropical eastern South America, Middle America and South Africa. More diversity in tropical eastern South America and West Indies.

XIV. South America: Includes 6 families, 2 of which belong to a subpattern. Distribution ranges through South America; usually extends to Middle America.

1. Orthalicidae (17). Tropical; primarily mainland. Relatively high diversity in tropical South America; some groups extend to Middle America.
2. Odontostomidae (16). Tropical to subtropical (extending to temperate); primarily mainland. Endemic to and relatively high diversity in South America; present in Fernando de Noronha islands; absent in western South America. (Miocene fossil in Florida.)
3. ? Systrophidae (14). Tropical to subtropical (extending to temperate); primarily mainland. Relatively high diversity in South America; 1 subgenus extends to Middle America.
4. Strophocheilidae (7). Tropical to subtropical (extending to temperate); mainland forms. Endemic to South America.

a) *Extended to Australia-Pacific:*

5. Bulimulidae (94). Tropical to subtropical (extending to temperate); primarily mainland. Very

highly diversified in South America; extend to Middle America and southwestern North America; some groups present in Galápagos, Australia and Pacific islands. Possible: southern distribution pattern.

6. Megaspiridae (5). (see XVIc.)

XV. *Australia-Pacific*: Includes 6 families, 2 of which belong to subpatterns. A highly endemic region. Distribution includes Australian and Pacific regions.

1. Amastridae (19). Tropical; island forms. Highly endemic; restricted to and highly diversified in Hawaiian islands.
2. Partulidae (12). Tropical; island forms. Endemic; restricted to and relatively diversified in high islands of Southern and Western Pacific.
3. Athoracophoridae (1). Tropical to subtropical (extending to temperate); equally distributed on mainland and islands. Endemic to Australia and South Pacific islands.
4. Otoconchidae (1). Subtropical to temperate; island forms. Highly endemic; found only in New Zealand.

a) *Extended to East Asia*:

5. Achatinellidae (23). Tropical to subtropical (extending to temperate); primarily island forms. Distribution includes Indo-Malayan, Austro-Malayan and Pacific islands; present also in Australia, New Zealand, Japan, Formosa, Galápagos and Juan Fernández islands. Relatively high diversity in Hawaiian islands.

b) *Extended to South Asia and East Asia*:

6. Trochomorphidae (24). Tropical (extending to subtropics and temperate); primarily island forms. Distribution ranges from Orient to Pacific regions; a few groups extend to Manchurian Palaearctic. Relatively high diversity in the Pacific islands.

XVI. *Southern Distribution*: Includes 4 families. This pattern encompasses all families with general distribution south of the equator; excluding those endemic to any particular continental mass or region.

a) *Madagascar-Ceylon-Australia and southern South America*:

1. Acavidae (12). Tropical to temperate; primarily island forms. Relatively diversified and distributed in Madagascar, Seychelles, Ceylon, New Guinea, continental Australia, Tasmania and Chile.

b) *South Africa-Australia-Pacific*:

2. Rhytididae (Paryphantidae) (19). Tropical to temperate; primarily island forms. Relatively diversified and distributed in South Africa, Seychelles, continental Australia, New Zealand, Tasmania, Borneo, Moluccas, New Guinea and Melanesian islands.

c) *Australia-South America*:

3. Megaspiridae (5). Tropical to subtropical; primarily mainland. Distributed in Brazil, New Guinea and Queensland (Australia). Possible: South America extended to Australia-Pacific subpattern. (Cretaceous to Oligocene fossils in Europe.)
4. Bulimulidae (94). (see XIVa.)

Notes:

1. The slug family Veronicellidae is considered by some authorities as forming a third order in Pulmonata, the Systellommatophora. Distribution of the Veronicellidae is Pantropical.

Veronicellidae (16). Tropical (extending to subtropics); primarily mainland. Pantropical in distribution. Relatively diversified and present in Africa, Orient, western part of continental Australia, South Pacific islands, Middle and South America.

2. Fossil families:

- a) ? Acroreidae (Basommatophora): restricted to North America in Cretaceous and Europe in Eocene.
- b) Payettiidae (Basommatophora): restricted to North America in the Miocene.
- c) ? Filholidae (Stylommatophora): restricted to Europe from Eocene to Oligocene.
- d) ? Anadromidae (Stylommatophora): restricted to Europe from Cretaceous to Eocene.

NUMERICAL ACCOUNT OF THE FAMILY DISTRIBUTION

Table 2 shows the number of genera and subgenera found in each of the 39 areas for each pulmonate family. When figures are plotted on a map, they give essentially

TABLE 2. Numerical account of family distributional ranges of pulmonate gastropods.

[illegible]

TABLE 3. Patterns of family distribution in pulmonate gastropods.

A. OLD WORLD-NEW WORLD PATTERNS:	B. OLD WORLD PATTERNS:	C. NEW WORLD PATTERNS:
I. <u>World-Wide:</u>	VI. <u>Africa-Orient-Palaeartic:</u>	XI. <u>North, Middle and South Amer.:</u>
1. Endodontidae (106) 2. Euconulidae (94) *3. Planorbidae (84) *4. Ellobiidae (55) 5. Vertiginidae (39) 6. Chondrinidae (34) *7. Lymnaeidae (34) 8. Pupillidae (27) 9. Succineidae (26)	25. Eridae (80)	47. Helminthoglyptidae (51)
a). <u>Nearly World-Wide:</u>	VII. <u>Palaeartic:</u>	XII. <u>North America:</u>
10. Clausiliidae (227) *11. Siphonariidae (19) 12. Valloniidae (19) *13. Ancyliidae (15) *14. Physidae (6) *15. Trimusculidae (1)	26. Pyramidulidae (1) —. (Helicidae) (192)	48. Polygyridae (34) 49. Haplotrematidae (8) 50. ?Ammonitellidae (5) *51. Lancidae (4) 52. Oreohelicidae (2)
II. <u>Pantropical:</u>	VIII. <u>Western Palaeartic:</u>	a). <u>Extended to Middle America:</u>
16. Streptaxidae (87) 17. Subulinidae (80)	27. Trigonochlamyidae (7) 28. Orculidae (5) 29. Parmacellidae (5) 30. Milacidae (4) 31. Testacellidae (3) *32. Otinidae (2) 33. Pleurodiscidae (1)	—. (?Thysanophoridae) (10)
a). <u>Extended to Western Palaeartic:</u>	a). <u>Extended to Siberian Palaeartic:</u>	XIII. <u>Middle America:</u>
—. (Ferrussaciidae) (20)	34. Helicidae (192)	53. Urocoptidae (79) 54. Sagdidae (21) 55. Oleacinidae (12) 56. Ceriidae (5)
III. <u>Holarctic:</u>	b). <u>Extended to the Tropics:</u>	a). <u>Extended to N. Amer.:</u>
18. Zonitidae (93) 19. Vitrinidae (14) 20. Cionellidae (14) *21. Acroloxidae (3)	35. Ferrussaciidae (20)	57. ?Thysanophoridae (10)
a). <u>Nearly Holarctic:</u>	c). <u>Extended to N. Amer.:</u>	b). <u>Extended to Mediterranean:</u>
22. Arionidae (24) —. (Limacidae) (26)	36. Limacidae (26)	58. Spiraxidae (44)
IV. <u>South and East Asia, Australian-Pacific, Middle and South America:</u>	IX. <u>Africa:</u>	c). <u>Extended to S. Africa:</u>
23. Camaenidae (94)	37. Urocyclidae (44) 38. Achatinidae (23) 39. Dorcasidae (3) 40. Aillyidae (1) 41. Chlamydephoridae (1) 42. ?Thyrophorellidae (1)	59. Amphibulimidae (8)
V. <u>East Asia-America:</u>	X. <u>East Asia-Africa:</u>	XIV. <u>South America:</u>
24. Philomycidae (1)	43. Bradybaenidae (80) 44. Corillidae (8)	60. Orthalicidae (17) 61. Odontostomidae (16) 62. ?Systrophidae (14) 63. Strophochelidae (7) *64. Chinidae (1)
—. <u>Middle America to Parts of Old World:</u>	a). <u>Extended to Australian-Pacific:</u>	a). <u>Extended to Australian-Pacific:</u>
a). <u>Middle America extended South Africa:</u>	45. Ariophantidae (73) 46. Helicarionidae (69)	65. Bulimulidae (94) —. (Megaspiridae) (5)
—. (Amphibulimidae) (8)	D. AUSTRALIAN-PACIFIC PATTERNS:	E. SOUTHERN DISTRIBUTION PATTERNS:
b). <u>Middle America extended to Mediterranean:</u>	XV. <u>Australian-Pacific:</u>	XVI. <u>Southern Distribution:</u>
—. (Spiraxidae) (44)	66. Amastridae (19) 67. Partulidae (12) 68. Athoracophoridae (1) 69. Otoconchidae (1) *70. Latiidae (1)	a). <u>Madagascar-Ceylon-Australia and southern South America:</u> 74. Acavidae (12)
	a). <u>Extended to East Asia:</u>	b). <u>S. Africa-Australia:</u>
	71. Achatinellidae (23) *72. Amphibolidae (2)	75. Rhytididae (19)
	b). <u>Extended to South Asia and East Asia:</u>	c). <u>Australia-South Amer.:</u>
	73. Trochomorphidae (24)	76. Megaspiridae (5) —. (Bulimulidae) (94)

the family distribution range, together with an index of diversity in different parts of the range.

An important added function of the table is to make cross reference possible. Reading horizontally (to the areas or regions), one can readily determine the pulmonate families that can be expected in any one area, subregion or region of the world.

The families are arranged in systematic sequence as presented by Taylor & Sohl (1962), beginning with the 1st basommatophoran family, the Trimusculidae, and ending with the last stylommatophoran family, the Helicidae.

PATTERNS OF FAMILY DISTRIBUTION

Based on Zilch's raw distribution data, the pulmonates show 16 major family distribution patterns and several subpatterns, which in Table 3 are placed into 5 convenient groups: Old-World-New-World Patterns; Old-World Patterns; New-World Patterns; Australian-Pacific Patterns; and Southern Distribution Patterns. The 16 distribution patterns represent a refinement of the 12 patterns reported earlier by the author (Te, 1972). This refinement was brought about by the more exact quantification of data in the present study. In the main, however, the earlier version agrees quite well with the current system.

Table 3 shows the distribution patterns, as well as the families exhibiting each pattern. Parentheses around a family name indicate the possibility of its being included in a particular pattern, but the family is actually classed under another pattern. Basommatophoran families are indicated by an asterisk (*). The total number of genera and subgenera found in each family is given in parentheses after each family name and indicates the relative size and diversity of the family.

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SELECTIVE SITE SEGREGATION IN *BALCIS SHAPLANDI* AND
MUCRONALIA FULVESCENS (MOLLUSCA: GASTROPODA: AGLOSSA)
PARASITIC UPON *ARCHASTER TYPICUS* (ECHINODERMATA: ASTEROIDEA)

Brian Morton

ABSTRACT

Mucronalia fulvenscens and *Balcis shaplandi* are found in Hong Kong waters to be parasitic upon the littoral asteroid *Archaster typicus*, an inhabitant of sandy shores at extreme low water. Only a very small percentage of the population of starfish (0.03%) possesses both parasites, thereby exhibiting partial spatial separation.

Even when occurring on the same host, moreover, the location of the parasites is highly specific and they exhibit the phenomenon of selective site segregation which, as far as is known, is undescribed for any other molluscan parasites. *Mucronalia fulvenscens* is cream coloured and attaches to the in-framarginal plates in the oral inter-radius of the arms. It superficially closely resembles the flattened marginal spines. *Balcis shaplandi* is grey-green in colour and flecked with brown. It resembles the colour of the aboral surface of the arms where it characteristically occurs, typically at the extremities. The 2 species of parasites are thus diametrically segregated on the same host. The position of both is possibly regulated, in part, by the copulatory activity of the host.

A 3rd symbiont, the commensal hesionid annelid *Podarke angustifrons*, occasionally occurs in the ambulacral grooves.

INTRODUCTION

The principle of Gause (1934) of 1 species to a niche draws wide support from parasitology, particularly with regard to endoparasites and a phenomenon referred to by Inglis (1971) as intra-host diversification and by Holmes (1973) as selective site segregation. For example, different nematodes occupy different sites within the gut of the European tortoise (*Testudo graeca*) (Schad, 1963; Petter, 1966), and Madsen (1945) has shown that different species of *Capillaria* can co-occur in birds. Similarly, 2 liver flukes, *Fasciola hepatica* and *Fascioloides magna*, occupy somewhat different sites in the liver and may co-exist in cattle (Olsen, 1949; Foreyt & Todd, 1972). No fewer than 5 species of cyclophyllideans occupy overlapping zones in the intestine of the shrew *Sorex araneus* (Lewis, 1966). Much of the literature relating to selective site segregation in helminths has been reviewed by Holmes (1973). For other endoparasites comparable data are available, although for ectoparasites, with the exception of the Insecta and Arachnida (Dubinin, 1948, 1951), relatively less data exist. This is particularly true of the ectoparasitic Mollusca.

In the Indo-Pacific, many echinoderms are characteristically parasitised by members of the molluscan superfamily Aglossa (Franc, 1968). The specific families concerned are the Eulimidae (= Melanellidae), Paedophoropodidae, Stiliferidae, Asterophilidae and Entoconchidae. Members of the Pyramidellidae seem to favour annelids and molluscs as hosts (Fretter & Graham, 1949). Much of the literature pertaining to these specialised molluscs has been reviewed by Koehler & Vaney (1912), Vaney (1913), Pelseneer (1928) and Habe (1952).

Some aglossans are specialised endoparasites, e.g., *Megadenus holothuricola* in the respiratory trees of *Holothuria mexicana* (Rosen, 1910). Others are less specialised ectoparasites and although most occur on a single host, e.g., *Curveulima aurata* on *Anthocidaris crassispina* and *Cuspieulima peronellicola* on *Peronella japonica* (Habe, 1952), others may occur on 2 hosts, e.g., *Melanella astropectenicola* on *Astropecten polyacanthus* and *Luidia maculata* (Habe, 1952; Hyman, 1955). Yet others may occur as mixed populations on the same host, e.g., *Rosenia yamamotoi* and *R. lokiokai* on *Diadema setosum* (Habe, 1952) and *Melanella astropectenicola* and *M. robusta* on *Astropecten polyacanthus* (Hyman, 1955). Most authorities have neglected to specify the exact location of such parasites, beyond generalised references to the oral or aboral surface.

The intertidal starfish *Archaster typicus* (Müller & Troschel) is parasitised by the molluscs *Balcis shaplandi* Melvill (Eulimidae) and *Mucronalia fulvescens* (A. Adams) (Stiliferidae), which exhibit a nice example of selective site segregation on their echinoderm host. This association, from a population of *A. typicus* inhabiting Tai Tam Bay, Hong Kong, is described below.

MATERIALS AND METHODS

In April, 1973, 396 specimens of *Archaster typicus* were collected from extreme low water levels on a sandy shore in Tai Tam Bay, Hong Kong. Each was measured to the nearest mm from the tip of one arm to the inter-radius of the 2 opposite arms. Specimens of *Balcis shaplandi* and *Mucronalia fulvescens*, where present, were removed, and their exact location on their host was plotted on prepared diagrams using the madreporite as a standard reference point. The numbering of the arms and the inter-radii followed the scheme proposed by Hyman (1955). The occurrence of the parasites in groups or as separate individuals was also noted.

RESULTS

An analysis of the parasite population

The population of *Archaster typicus* inhabiting Tai Tam Bay in April, 1973 apparently comprised a single age class, the mean size being between 80–85 mm from the tip of one arm to the opposite inter-radius. Of the 396 specimens examined, a total of 125 (31.6%) possessed 1 or more individuals of 1 or both species of parasite. Altogether, 78 *Mucronalia fulvescens* and 129 *Balcis shaplandi* were recorded, i.e., an infection rate of approximately 20% and 33% respectively. Of these, a total of 72 specimens of *M. fulvescens* were located upon 63 starfish, i.e., an average infestation of 1.14 per starfish. A total of 104 specimens of *B. shaplandi* were located upon 75 starfish, i.e., an average infestation of 1.39 per starfish. The remaining 31 parasites had become separated from their hosts and were not included in this analysis. Only 13 starfish (0.03% of the population) possessed both species of parasite.

An analysis of the number of specimens of *Mucronalia fulvescens* per host reveals that 56 starfish possessed 1 parasite (77.7%), 6 starfish possessed 2 parasites (16.7%), and 1 starfish possessed 4 parasites (5.6%). Of the 12 parasites which occurred as 2 individuals on the one host, 10 were in pairs and 2 were solitary individuals located in different positions on the same host. Of the 4 parasites which occurred on 1 starfish, 2 were a pair and the other 2 were solitary. Thus, of the number of specimens of *M. fulvescens*, 60 occurred as solitary individuals (83.3%), while 12 occurred in 6 groups of 2 (16.7%).

An analysis of the number of specimens of *Balcis shaplandi* per host reveals that 54 starfish possessed 1 parasite (51.9%), 14 starfish possessed 2 parasites (26.9%),

6 starfish possessed 3 parasites (17.3%), and 1 starfish possessed 4 parasites (3.8%). Of the 28 parasites which occurred as 2 individuals on 1 host, 18 occurred in pairs and 10 were solitary individuals located in different positions on the same host. Of the 18 parasites which occurred as 3 individuals on the same host, 15 were in triads while 3 others occurred as solitary individuals. The 4 individuals found on 1 host were grouped together in a tetrad. Thus, of the total number of specimens of *B. shaplandi*, 67 occurred as solitary individuals (64.4%), 18 occurred in 6 groups of 2 (17.3%), 15 occurred in 5 groups of 3 (14.4%), and 4 occurred in 1 group of 4 (3.8%). Thus, 35.6% of all individuals of *B. shaplandi* occurred with at least 1 other individual.

Location on the host

As mentioned previously, only 0.03% of the population of *Archaster typicus* was parasitised by individuals of both species of parasite. The distribution of both species of parasite was found to be uniform throughout the size range of the starfish population: the frequency peaks of both parasites coincide and correspond with the frequency peak of the host. Thus, there seems to be no temporal separation of the parasites within the population of starfish on a size basis.

Mucronalia fulvescens is cream in colour and was most commonly found attached to the elongate infra-marginal plates of the host close to the inter-radius of the arms (Fig. 1A). The infra-marginal plates are particularly long in *Archaster*. The fringing marginal spines interposed between the supra- and the infra-marginal plates are 2.5-3.0 mm long and are similarly cream coloured. As well as being coloured like the spines, *M. fulvescens* is furthermore extremely difficult, if not impossible, to discern when the starfish is viewed from above. Specimens of *M. fulvescens* have also been found in the ambulacral grooves, and sections of the animal *in situ* show that it is tapping the fluid content of the tube feet, i.e., the water vascular system.

Another symbiont, the commensal hesionid annelid *Podarke angustifrons* (Grube), was occasionally encountered, and it typically occurred within the ambulacral grooves.

Balcis shaplandi, living on the aboral surface of the starfish, is cryptically coloured, being grey-green flecked with brown and almost perfectly matches the aboral surface of the starfish. This species was always found (Fig. 1B) attached to either the supra-marginal, dorsolateral or to the carinal plates of the extremities of the arms. It erodes a circular patch of epidermis away to facilitate insertion of the proboscis into the coelom from which it draws fluids.

Of the 64 specimens of *Mucronalia fulvescens* whose position was accurately known, the numbers which occurred in each inter-radius were AB=10, BC=10, CD=19, DE=11 and EA=14. Of the 83 specimens of *Balcis shaplandi* which were actively feeding upon their host and whose position could thus be accurately fixed, the number which occurred on each of the 5 arms were A=24, B=12, C=17, D=14 and E=16. Possibly significantly, the greatest numbers of specimens of *M. fulvescens* (19) occurred in the inter-radius (CD) of the arms opposite the arm (A), which possessed the greatest number of specimens of *B. shaplandi* (24). The madreporite is also located in this axis.

Thus *Mucronalia fulvescens* and *Balcis shaplandi* exhibit the phenomena of partial spatial separation and selective site segregation.

DISCUSSION

Direct competition between species, whether parasitic or free living, may lead

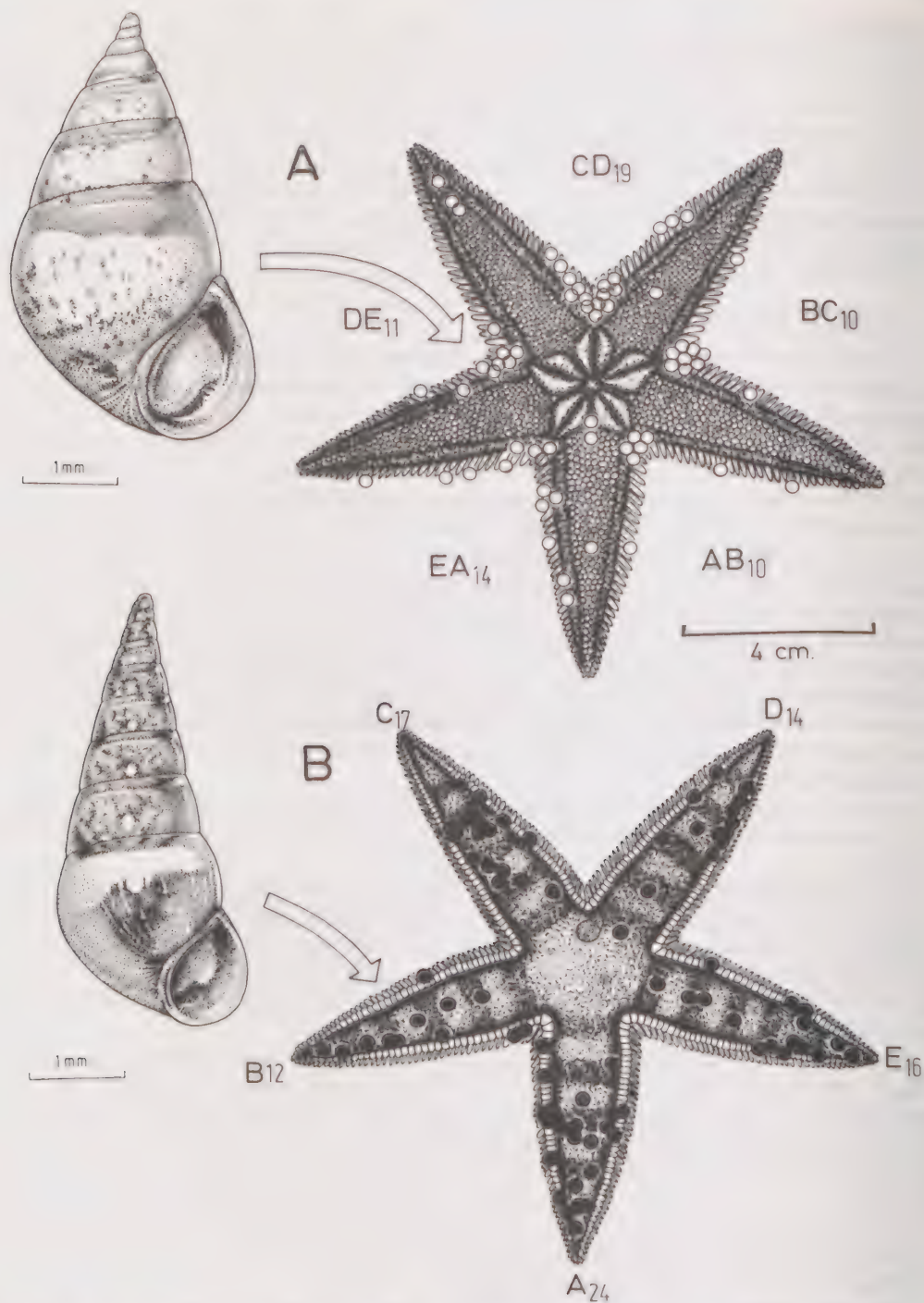


FIG. 1. The cumulative distribution of (A) *Mucronalia fulvescens* and (B) *Balciis shaplandi* upon *Archaster typicus* from Tai Tam Bay, Hong Kong. In A (ventral view), the inter-radii of the starfish arms are designated by the letters AB, BC, CD, DE and EA, and in B (dorsal view), the arms are designated by A, B, C, D and E. In both figures, subscript numbers indicate the number of parasites.

to the selective exclusion of one of them. Alternatively, by interaction, segregation of the species might occur, either temporally or spatially, leading in the latter case to specialisation and to a narrowing of both niches. Temporal segregation is found in the spiruroid nematodes *Cucullanus heterochrous* and *C. mintus*, which invade the intestine of flounders at different times of the year (MacKenzie & Gibson, 1970), and in the cestodes *Triaenophorus nodulosus* and *T. crassus*, which parasitise different age classes of pike (*Esox lucius*) (Miller, 1943). The population of *Archaster typicus* inhabiting Tai Tam Bay comprised a single age class in April; and no temporal segregation of its molluscan parasites occurs.

The low incidence of concurrent infestation seen in *Archaster typicus* would suggest that a partial spatial separation of the 2 parasites occurs, although how this is effected is unknown.

Most significantly, the distribution of *Balcis shaplandi* and *Mucronalis fulvescens* is influenced by selective site segregation. This phenomenon, best seen in endoparasites, is well exemplified wherever a detailed study of the exact location of the parasites has been made (Holmes, 1973). Thus, Schad (1963) and Petter (1966) were both able to demonstrate that up to 15 species of pinworms were selectively distributed along the gut of the European tortoise (*Testudo graeca*). Schad (1962) and Schad & Kuntz (1968) similarly reported that several species of *Kalicephalus* can occur within a single reptilian host. Wertheim (1970) showed that the nematodes *Strongyloides ratti* and *S. venezuelensis* occurred in the same region of the intestine of rats, but that the former was limited to the Crypts of Lieberkuhn, whereas the latter occurred on the villi. In ectoparasites too, Dubinin (1948) has shown that 3 groups of *Mallophaga* are restricted to definite areas of the plumage of *Ibis*, while Nikolskaya (1939) and Dubinin (1951) have shown that 3 species of tick are specifically located on different wing primaries of a cormorant.

Little is known of selective site segregation in the parasitic Mollusca, although different species are known to occur on the same host, e.g., *Odostomia unidentata* and *O. lukisii* on *Pomatoceros triqueter* (Fretter & Graham, 1949), *Rosenia yamamotoi* and *R. tokiokai* on *Diadema setosum* (Habe, 1952). *Melanella astropectenicola* and *M. robusta* on *Astropecten polyacanthus* (Hyman, 1955) and *Pseudoskenella depressa* and *Egila mayi* on *Galeolaria caespitosa* (Ponder, 1973). The 2 aglossan parasites of *Archaster* reported upon here are differently coloured in accordance with their separate niches and may also possess subtly different morphological adaptations of the suctorial structures, suiting them to their micro-habitat. Fretter & Graham (1949) regard the Aglossa as being essentially fluid feeders. Furthermore, the host may play a role in determining their distribution, since *Archaster typicus*, unlike the majority of starfish, copulates. In the spring, males may be found overlying the females, the arms of the 2 individuals alternating. Thus, the distribution of *Balcis shaplandi* could be limited to the extremities of the arms of the female starfish by the copulatory activity of the male. Similarly, *Mucronalia fulvescens* might be preferentially located in the oral inter-radius as an area of the female similarly not influenced by the attentions of the male.

The commensal hesionid annelid *Podarke angustifrons* would also seem to be segregated spatially from the 2 molluscan parasites and occurs in the ambulacral grooves. The same species has been reported by Jones (1964) to be also commensal upon *Pentaceros hedemanni*.

A reappraisal of those molluscan parasites cohabiting the same host might prove worthwhile; for single infestations it is well known that many, if not all, parasitic molluscs are site specific. Fretter & Graham (1949), referring to the Pyramidellidae, state that "this habit of restricting its occurrence to one special location appears to be characteristic of every species of the family." Certainly this is true

of commensal bivalve molluscs, where a detailed study has always revealed a site specificity hitherto unrealised (Morton, 1972, 1973).

Selective site segregation, associated as it must be with multiple invasions of the host (in evolutionary terms), is in itself indicative of a mature community, but more importantly, it is a mechanism which leads to further specialisation.

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LEECHES (ANNELIDA: HIRUDINEA) FOUND IN NORTH AMERICAN MOLLUSKS

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ABSTRACT

Aquatic leeches are important as parasites and predators of many groups of animals. Eleven species are reported living in North American snails and clams, 7 of which are known to behave as parasites, 2 are assumed to be parasitic, and the other 2 are not parasitic. In this paper these leeches are listed, a key is provided to the species, their known molluscan hosts are indicated, and aspects of their taxonomy are discussed.

Aquatic leeches are usually predators or parasites, and some have medical importance in that they serve as 1st and 2nd intermediate hosts, or as final hosts, of parasitic protozoans, trematodes, cestodes, nematodes and nematomorphs. In spite of the importance of leeches, knowledge of their ecology, distribution and taxonomy is wanting. One important aspect of the ecology of leeches is that their abundance and distribution appears to be regulated principally by the availability of food organisms. However, the diets of many species are unknown, inadequately reported, or appear questionable in light of recent studies by Soós (1969), Sawyer (1972) and Klemm (1975).

The feeding behavior of leeches is generally accepted as a form of predation. Nevertheless, their trophic level, i.e., whether they are predators, parasites or scavengers, is difficult to determine for many species. Past studies have indicated that most leeches are not host-specific but tend to restrict their diets to certain animal groups (e.g., insects, crustaceans, annelids, mollusks, frogs, salamanders, turtles, fishes, birds or mammals). J. P. Moore (1939) indicated that most of the smaller species of Glossiphoniidae are habitually malacophagous and that they feed almost exclusively on aquatic snails. Yet, in the family Glossiphoniidae in North America, only species of *Glossiphonia*, *Helobdella* and *Marvinmeyeria* are known to feed on mollusks, and some interesting snail-host preferences have been reported (J. E. Moore, 1964; Sarah, 1971; Klemm, 1973, 1975).

Species in the genera *Glossiphonia*, *Helobdella* and *Marvinmeyeria* have a proboscis which aids in sucking blood. In the sanguivorous process, not only all the body fluids of the snail host may be devoured, but also the tissues of the animal as well. This behavior can be considered as predation. Nevertheless, young individuals of some species may live for awhile inside their molluscan hosts, taking only an occasional blood meal (Wilkialis, 1964; Gruffydd, 1965; Hatto, 1968; Sarah, 1971; Klemm, 1972a, 1973, 1975). This mode of nutrition can be termed parasitism.

The distribution of Glossiphoniidae is nearly world-wide and the family includes 22 genera, approximately 140 nominal species and several subspecies (Soós, 1966, 1969, 1970). The zoogeography of the species varies, some being common and cosmopolitan, while others are rare and have restricted distributions (see Soós, 1969, 1970 for distribution world-wide and Klemm, 1972b; Sawyer, 1972; Davies, 1973 for North America). Some species are endemic to 1 locality, and others appear

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restricted to 1 particular type of habitat. Most data on their distribution, however, are quite incomplete since many regions of the world have not been sampled adequately.

The present account contains new and more precise information (Table 1) on the diets of glossiphoniid leeches that feed primarily on mollusks, discusses aspects of leech taxonomy, and presents a taxonomic key to the leeches known from North American mollusks.

Two main glossiphoniid genera in North America, *Glossiphonia* and *Helobdella*, include species known to feed on mollusks (J. E. Moore, 1964; Sarah, 1971; Sawyer, 1972; Klemm, 1972a, 1973, 1975) and on other invertebrates (Klemm, 1972a, 1975; Sawyer, 1972).

Glossiphonia is represented in North America by 3 widely distributed species, *G. complanata*, *G. heteroclita* and *G. swampina*, and 1 subspecies, *G. complanata mollissima* (J. P. Moore, 1898; Pinto, 1923; J. P. Moore and Meyer, 1951; Klemm, 1972b; Sawyer, 1972, 1973). *G. complanata* and *G. heteroclita* also occur throughout Eurasia (Soós, 1966, 1969), while *G. swampina* is presently known only from the Carolinas in North America. The subspecies, *G. complanata mollissima*, is reported from Alaska (Bering and Kodiak Islands) by J. P. Moore (1898), Pinto (1923) and J. P. Moore & Meyer (1951). This questionable geographical subspecies is currently thought to be merely a color variant of *G. complanata* (Autrum, 1936; Sawyer, 1972).

Glossiphonia complanata is common in North America and is predominately a predator of mollusks (Klemm, 1975), although it has been reported by various authors to feed occasionally on other invertebrates. *G. heteroclita* is considered to be rare in North America (Klemm, 1972a, 1972b, 1975; Sawyer, 1972; Davies, 1973), but it probably is frequently overlooked because of its small size and inconspicuous coloration. In Europe, it has been reported to feed on various snails (e.g., Guibe, 1936; Gruffydd, 1965; Hatto, 1968). In North America, Klemm (1975) found it parasitizing the snail *Physa gyrina*, its only known host in the New World.

The rediscovery of another rare leech, *Glossiphonia swampina*, by Sawyer (1973) in the Coastal Plain of South Carolina and by Sawyer (pers. comm.) in North Carolina extends the range of the *heteroclita-swampina* complex in North America. The arrangement of the 3 pairs of eyes of *G. swampina* resembles that of *G. heteroclita*; however, *G. swampina* differs from *G. heteroclita* in having 4 to 7 mid-dorsal, irregular, transverse bars composed of small, blackish chromatophores. Also, *G. heteroclita* is reported to be a northern species (Sawyer, 1973), known only as far south as northwestern Pennsylvania (J. P. Moore, 1906) and northern Indiana (J. P. Moore, 1920). Extensive collecting from states with poorly known leech representation could extend the range of both. Sawyer (1972) also disclosed that generally the body of *G. heteroclita* is whitish and usually devoid of pigment, but that some specimens have 1 to 6 inconspicuous, fine, black chromatophores in sparse clusters situated metamerically from the cephalic end to the anal region, especially along the mid-dorsal line and along the margins of the posterior part of the body. Many specimens collected in benthic samples from the Great Lakes region have a dark to light brownish-black, solid or irregular, median stripe extending from the cephalic region posteriad. Also this pigmented stripe is sometimes interrupted. The dorsum may or may not bear inconspicuous brownish-black chromatophores in sparse clusters, especially in the posterior part of the body, including margins. Sawyer (1973) recommended that a more detailed morphological comparison of these 2 species is needed but that in the interim Bosc's (1802) *G. swampina* should be recognized as a valid species. Nonetheless, the taxon may belong in a disjunct population of a color variant of *G. heteroclita* or a very close species (J. P. Moore, 1952). Its feeding behavior is unknown, but the close morphological resemblance

of *G. swampina* to *G. heteroclita* suggests that its food preference may be snails.

The distribution of *Helobdella* is world-wide and many of the species prey upon freshwater invertebrates, some preferring mollusks. Apparently this genus has its center of distribution in South America (Sawyer, 1972), since more than 21 species and subspecies are known from Central and South America (Weber, 1913, 1915; Pinto, 1923; Autrum, 1936; Cordero, 1937; Ringuelet, 1943, 1944a, 1944b, 1945). Of the 29 species and several subspecies in this genus reported by Soós (1969) for the world, only 7 are known from North America (J. P. Moore, 1959; Klemm, 1972a, 1972b, 1975; Sawyer, 1972).

The validity of a number of *Helobdella* species remains uncertain. In the New World, some species names are in doubt because of the problem of polymorphism commonly observed in the *H. triserialis* complex in South America and the *H. fusca* complex in North America. The occurrence of intergrades and the variability in the degree of sensillae, papillation and pigmentation from one locality to another has caused some of the taxonomic confusion. Ringuelet (1943, 1944a, 1944b, 1945) examined many of the South American *Helobdella* and recognized 17 species and 5 subspecies of *H. triserialis*, of which at least 1, *H. triserialis lineata*, clearly belongs to the *fusca* group in North America (J. P. Moore, 1901; Sawyer, 1967, 1972). Ringuelet (1943) also regarded *H. lineata* as a variety of 1 extremely variable and widely distributed species, *H. triserialis*. J. P. Moore (1906) examined the *fusca* group and distinguished 3 varieties, *fusca*, *lineata* and *papillata*. At first he believed that these forms were probably connected by an overlap of morphological characters, but later he (1952, 1959) recognized each of these as distinct species. Of the 3 species, *H. papillata*, *H. lineata* and *H. fusca*, the last 2 are considered the most variable.

Sawyer (1972) in his critical review of North American *Helobdella* indicated that in some published records *H. fusca* is confused with *H. lineata*. Typically, *H. fusca* lacks dorsal papillae (Castle, 1900) and has longitudinal white stripes, alternating with coffee-brown stripes and/or lines, but lacks a transverse pattern. Also, *H. fusca* may have small metameric white spots in the anal region, resembling those found on *H. lineata*. The latter, on the other hand, has few, scattered or 3 series of black-tipped papillae, with or without longitudinal stripes, lines and 6 or fewer series of roundish metameric white spots. These spots are sometimes variable and may disappear in preserved specimens. Occasionally, in specimens in which the papillae are absent and the color uniform, *H. lineata* may be distinguished from *H. fusca* by the series of metameric white spots on the dorsum instead of the continuous longitudinal stripes. On very rare occasions, some specimens of the 2 species may be difficult to separate. *H. papillata*, on the other hand, is easy to identify by its numerous large papillae (arranged in 5, 7 or 9 longitudinal rows) that protrude from the dorsum.

On the bases of the arrangement of chromatophores, sensillae, and the presence of small papillae, J. P. Moore (1939) described a 4th related species, *Helobdella punctatolineata*. This species occurs commonly in Puerto Rico (J. P. Moore, 1939) and in the Dominican Republic (Klemm, unpubl.). Several reports of the species in the United States (Sapkarev, 1968; Klemm, 1972b; Richmond, 1972) remain questionable. However, specimens which closely resemble this species have been found recently from southern Lake Michigan (Klemm, unpubl.). Additional collecting may extend the known range of *H. punctatolineata*, or experimentation may demonstrate that individuals which resemble this species in North America are, in fact, a color variant of either the polymorphic *H. fusca* or *H. lineata*.

I have found the intensity and longitudinal arrangement of the brown or gray chromatophores to vary in some adult and young specimens collected from Puerto Rico and the Dominican Republic. Typically, the dorsum in both live and preserved adult

TABLE 1. Hosts cited in the literature of leeches (Glossiphoniidae) feeding on North American mollusks (including hosts reported in other regions of the world).¹

Hosts	Leech genera & species	Leech distribution
Mollusks, Oligochaetes, Insect larvae	<i>Glossiphonia</i>	World-wide
Mollusks: <i>Ancylus fluviatilis</i> <i>Bithynia tentaculata</i> <i>Gyraulus parvus</i> <i>Helisoma anceps</i> <i>Helisoma campanulatum</i> <i>Helisoma trivolvis</i> <i>Hydrobia jenkinsi</i> <i>Lampsilis siliquoidea</i> <i>Lymnaea stagnalis</i> <i>Promenetus exacuus</i> <i>Physa fontinalis</i> <i>Physa gyrina</i> <i>Physa heterostrophia</i> <i>Physa integra</i> <i>Planorbis corneus</i> <i>Planorbis vortex</i> <i>Pisidium</i> sp. <i>Sphaerium simile</i> <i>Sphaerium transversum</i> <i>Stagnicola reflexa</i>	<i>G. complanata</i>	Cosmopolitan, Holarctic Region, (Argentina ?), Europe, North America, India, Zaire
Snails: <i>Ancylus</i> sp. <i>Bithynia tentaculata</i> <i>Enchytracus albidus</i> <i>Leptolimnaea glabra</i> <i>Lymnaea stagnalis</i> <i>Pachylabra maura</i> <i>Physa fontinalis</i> <i>Physa gyrina</i> <i>Physa heterostrophia</i> <i>Planorbis contortus</i> <i>Planorbis corneus</i> <i>Planorbis nitidus</i> <i>Planorbis umbilicatus</i> <i>Radix pereger</i>	<i>G. heteroclita</i>	Holarctic Region, Europe, North America, India, Central and East Africa
Snails (unknown)	<i>G. swampina</i>	U. S. A. (North Carolina, South Carolina)
Mollusks, Oligochaetes, Insect larvae, Crustaceans	<i>Helobdella</i>	World-wide
Oligochaetes, Insect larvae, Snails (?)	<i>H. elongata</i>	North America

TABLE 1. (Cont.)

Hosts	Leech genera & species	Leech distribution
Mollusks: <i>Australorbis glabratus</i> <i>Helisoma anceps</i> <i>Helisoma campanulatum</i> <i>Helisoma trivolvis</i> <i>Lymnaea stagnalis</i> <i>Promenetus exacuus</i> <i>Physa gyrina</i> <i>Physa integra</i> <i>Physa parkeri</i> <i>Pisidium virginicum</i> <i>Stagnicola reflexa</i>	<i>H. fusca</i>	North, Central, South America
Snails: <i>Helisoma anceps</i> <i>Helisoma campanulatum</i> <i>Helisoma trivolvis</i> <i>Physa gyrina</i>	<i>H. lineata</i>	North, Central, South America
Snails: <i>Bulinnea megasoma</i> <i>Gyraulus parvus</i> <i>Helisoma anceps</i> <i>Helisoma campanulatum</i> <i>Helisoma trivolvis</i> <i>Physa gyrina</i> <i>Physa parkeri</i> <i>Stagnicola elodes</i>	<i>H. papillata</i>	Northern North America
Snails: <i>Australorbis glabratus</i> <i>Planorbis corneus</i> <i>Stenophysa marmorata</i>	<i>H. punctatolineata</i>	Puerto Rico, Dominican Republic, U. S. A. (?)
Oligochaetes, Insect larvae, Crustaceans, Mollusks (?)	<i>H. stagnalis</i>	Cosmopolitan, except Australia
Mollusks (highly doubtful): <i>Cincinnatia emarginata</i> <i>Promenetus exacuus</i> <i>Physa gyrina</i> <i>Physa integra</i> <i>Planorbis albus</i> <i>Pisidium</i> sp. <i>Sphaerium transversum</i> <i>Stagnicola reflexa</i>		

TABLE 1. (Cont.)

Hosts	Leech genera & species	Leech distribution
Snails (unknown)	<i>H. transversa</i>	U.S. A. (Southern Michigan)
Snails:	<i>Marvinmeyeria</i>	North America
<i>Aplexa hypnorum</i>	<i>M. lucida</i>	Northern North America
<i>Gyraulus parvus</i>		
<i>Helisoma trivolvis</i>		
<i>Physa gyrina</i>		
<i>Physa heterostrophia</i>		
<i>Planorbula armigera</i>		
<i>Promenetus exacuus</i>		
<i>Stagnicola elodes</i>		
<i>Stagnicola emarginata</i>		
<i>Stagnicola exilis</i>		

¹From Klemm, 1974.

and young bears longitudinal brown or gray lines (singly and doubly arranged) and 4 to 6 transverse rows of white spots (sensillae) on every sensory annulus, giving an effect of alternating longitudinal light and dark lines. In some individuals the intensity and distribution of the brown or gray pigments vary. In most specimens a median stripe extends from the eyes to the anus. It is darker than the other longitudinal lines and the pigmentation tends to be concentrated at the margins of the stripe leaving the middle paler. In some instances, the demarcation is so obvious that the median stripe appears divided into a pair of brown to gray lines. On the sensory annuli of most specimens, a series of 4 to 6 white spots extends transversely over the entire body. The median spots are the largest and are lateral to the median stripe. Posteriad they expand into roundish spots. In both live and preserved specimens of some adults and young, the white spots may be variable or missing. Usually the dorsum of the sensory annulus of each somite contains a few small but somewhat staggered distinct papillae. Those on the median stripe are the largest and usually tipped with black pigment. Occasionally, on some individuals, the papillae are barely visible or not discernable.

Sawyer (1972) added yet a 5th species, *Helobdella transversa*, which he collected from southern Michigan. Its description is based primarily on the arrangement of the transverse rusty-brown and alternating metameric white bands, which consist of 8 to 10 slightly raised white spots in various states of confluence. In contrast to *H. fusca*, *H. transversa* has no longitudinal pattern of white and brown stripes.

Based on the interpretation of Soós (1969), Davies (1971) relegated *Helobdella fusca* and *H. lineata* to the synonymy of *H. triserialis*. *H. papillata*, however, was retained as a distinct species (Soós, 1969). Klemm (1972a, 1972b, 1975) and Sawyer (1972) have often collected *H. fusca*, *H. lineata* and *H. papillata*, and consider these 3 to be consistently recognizable forms (i.e., distinct species). In addition, Sawyer (1972) found 2 questionable forms of *H. fusca* (one being a whitish form lacking pigmentation and the other being a mottled form, pigmented with irregularly

spaced whitish blotches on a brownish background and with no longitudinal stripes or bands). Until the problem of polymorphism in the *fusca* complex is settled by laboratory rearing, the names for the American *Helobdella* will not be finally settled. Therefore, in this paper the nomenclature of J. P. Moore (1959) is followed.

Further, an important problem with respect to the family Glossiphoniidae and the genus *Helobdella* is the insufficient amount of distributional data and the lack of well-defined species characters for some of the common as well as the poorly known forms. Until better taxonomic characters are established by a detailed study of the anatomical features, the status of several *Helobdella* species will remain questionable. In North America, this is especially true for the *fusca* complex in which the variability of the papillae, sensillae and arrangement of the chromatophores causes confusion. Also, the clarification of taxonomic and zoogeographical problems in *Helobdella* and in some of the other genera of leeches is hampered by the lack of comparative ontogenetical, embryological and genetic studies (Soós, 1970). A number of species currently recognized almost exclusively on their external morphological features may have been incorrectly classified.

Helobdella fusca, *H. lineata*, *H. papillata* and *H. punctatolineata* have been reported to feed primarily on mollusks (e.g., J. P. Moore, 1939; Harry & Aldrich, 1958; McAnnally & D. V. Moore, 1966; Sarah, 1971; Klemm, 1972a, 1975; Sawyer, 1972). The feeding habit of *H. transversa* is unknown (Sawyer, 1972), but since the animal is closely related morphologically to the above species, it may also be malacophagous.

Two other species of Glossiphoniidae, *Helobdella elongata* and *H. stagnalis*, have poorly known feeding requirements, and their feeding on mollusks is doubtful (Sawyer, 1972; Klemm, 1975). *H. stagnalis* is the only North American species of leech with a brown chitinous scute in the anterior region. On rare occasions when the scute is missing, the species might be confused with *H. elongata*. Posteriorly, *H. stagnalis* is relatively wider than *H. elongata*, whose body has a cylindrical worm-like appearance and whose body margins are nearly parallel. *H. stagnalis* has 6 pairs of crop caeca, whereas *H. elongata* has only 1 pair.

Marvinmeyeria [= *Oculobdella*] (also Glossiphoniidae) is represented in North America by 1 species, *M. lucida*. Soós (1969) erected the genus *Marvinmeyeria* based on the configuration of the posterior end of its reproductive organs, which differ from those in the type species, *Oculobdella socimulcensis* Caballero 1931 (known only from Mexico). Meyer & J. P. Moore (1954) had indicated that a new genus would probably have to be established for *M. lucida*. This poorly known species is often encountered in woodland pools and temporary or semipermanent bodies of water in Michigan (Sawyer, 1968, 1972; Klemm, 1972a, 1973, 1975) and in various habitats in Canada (Meyer & J. P. Moore, 1954; J. E. Moore, 1964, 1966; Davies, 1973). *M. lucida* feeds only on snails (J. E. Moore, 1964; Klemm, 1972a, 1973, 1975). In adult and young specimens, the dorsal and ventral surfaces are heavily pigmented with uniform blackish-gray chromatophores and with thin, dark, paramedial lines prevalent in the anterior region. On a few occasions young were observed to be uniformly white and lacking the dusky, blackish-gray pigments.

Another glossiphoniid species, *Placobdella montifera*, has been recorded in mussels (J. P. Moore, 1912) and has been reported by various authors to feed on or attach to other invertebrates, amphibians and fishes. However, the only confirmed host records have been from a variety of fishes (Ryerson, 1915; Pearse, 1924; Bere, 1931; Bangham, 1933; Bangham & Hunter, 1939; Harms, 1959, 1960; Hoffman, 1967; Poe, 1972; Richmond, 1972; Klemm, unpubl.). Reports of its feeding on mussels are doubtful; hence, the species is not included in this study, but it

can be identified by using one of several other keys (J. P. Moore, 1959; Davies, 1971; Klemm, 1972b; Sawyer, 1972). Wilson & Clark (1912) and Coker *et al.* (1921) also found leeches in mussels (i.e., in the mantle cavity) and believed they ate the mussel's mucus. Some leeches are often found attached to both vacant and occupied shells of mussels, but they probably use the shells only as a substrate for attachment.

The leeches in this paper, i.e., those found associated with freshwater mollusks, can be identified by a number of features. The key which follows was constructed from characters observed in living and preserved specimens, both young and adult, and includes their known distributions. In regard to *Helobdella fusca*, *H. lineata* and *H. punctatolineata*, some allowances should be made for morphological variability when using the key.

Key to leeches found in North American mollusks

- 1a. Eyes 1 pair, always separated (Fig. 1) 2
 1b. Eyes 3 pairs (Fig. 2a,b). Genus *Glossiphonia* 9



Fig. 1



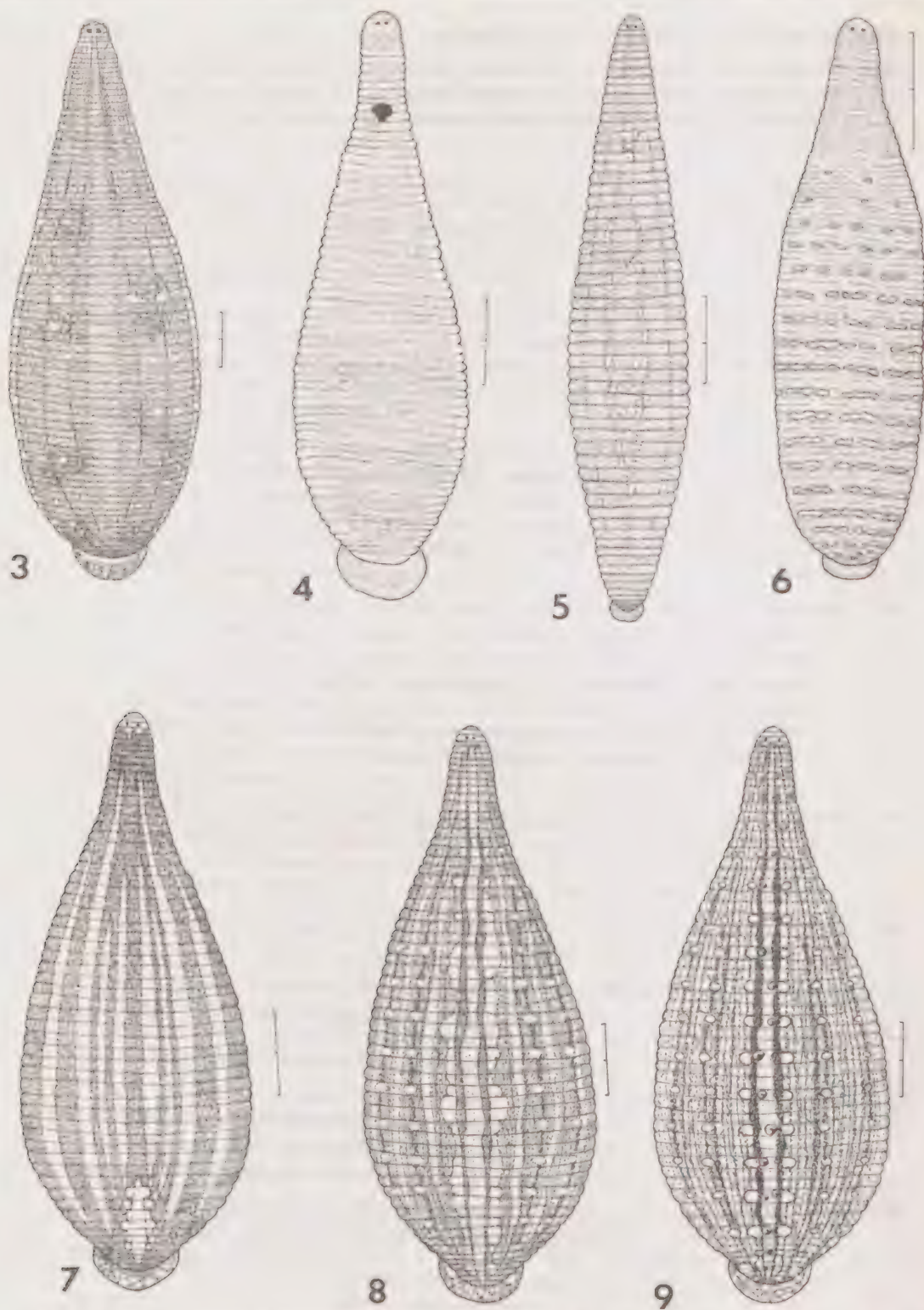
Fig. 2a



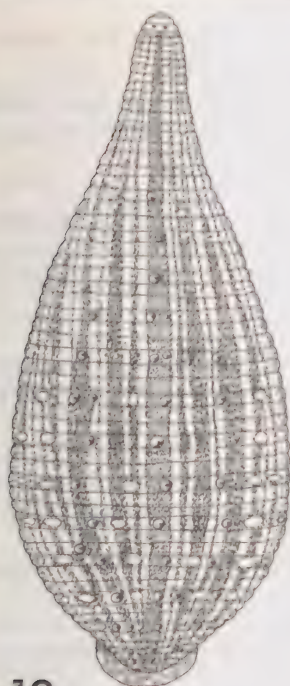
Fig. 2b

- 2a. Dorsum unpigmented, uniformly pigmented, or pigmented with longitudinal or transverse bands, lines or stripes and with or without metameric whitish spots (sensillae) on every 3rd annulus in middle of body region; heavily to sparsely or not papillated, or with a chitinous scute (nuchal plate) in anterior region; gonopores separated by at least 1 annulus. Genus *Helobdella* 3
 2b. Dorsal and ventral surfaces heavily pigmented with uniform, minute, blackish chromatophores, with thin dark paramedial lines extending into anterior region; dorsal surface smooth, no papillae or scute; gonopores united; uncommon, but locally abundant in northern North America. (Fig. 3) *Marvinmeyeria* [= *Oculobdella*] *lucida* (Moore 1954)
 3a. Without a chitinous scute in the anterior region 4
 3b. With a chitinous scute on dorsum in the anterior region; cosmopolitan. (Fig. 4) *Helobdella stagnalis* (Linnaeus 1758)
 4a. Dorsum smooth, without papillae 5
 4b. Dorsum with papillae (few, scattered, or arranged in 3 to 9 longitudinal rows on neural annuli) 8
 5a. Body pigmented, with or without longitudinal or transverse bands, lines and/or stripes; body flat; usually 6 pairs of crop caeca 6
 5b. Body unpigmented, elongate and subcylindrical; lateral margins of body almost parallel, body smoothly round; posterior sucker small, terminal; translucent; 1 pair of crop caeca; uncommon, but locally abundant in North America. (Fig. 5) *Helobdella elongata* (Castle 1900)

- 6a. Dorsum without transverse pigmentation 7
- 6b. Dorsum with transverse rusty-brown, interrupted bands alternating with irregular whitish bands, the latter consisting of 8 to 10 confluent white metameric spots on each neural annulus; **uncommon**, known only from southern Michigan. (Fig. 6) *Helobdella transversa* Sawyer 1972
- 7a. Color uniform coffee-brown *or* with longitudinal whitish stripes alternating with coffee-brown stripes and/or lines; with or without small whitish spots in anal region; a variable species; common in northern North America, occurs also in southern United States. (Fig. 7) *Helobdella fusca* (Castle 1900)
- 7b. Dorsal pigmentation brown or gray, arranged in numerous longitudinal stripes or lines; neural annuli with 4 to 6 longitudinal rows of whitish spots over entire body; common in Puerto Rico and Dominican Republic, occurrence in North America questionable. (Fig. 8) *Helobdella punctatolineata* Moore 1939
- 8a. Dorsum with sparse, small, brown to black papillae, largest and most numerous on the median stripe; pigmentation brown or gray, arranged in numerous longitudinal stripes or lines; neural annuli with 4 to 6 longitudinal rows of whitish spots over entire body; common in Puerto Rico and Dominican Republic, occurrence in North America questionable. (Fig. 9) *Helobdella punctatolineata* Moore 1939
- 8b. Dorsum with 3 rows (typically) or fewer of small, black-tipped or uniformly pale papillae; pigmentation arranged in numerous longitudinal light and dark lines and/or stripes; whitish spots on neural annuli, unaligned or if aligned, then confined to areas lateral to papillae (Fig. 10) *or* color uniform with papillae few, scattered, or in 3 rows; whitish spots on neural annuli unaligned or aligned (Fig. 11); a variable species; common in North America *Helobdella lineata* (Verrill 1874)
- 8c. Dorsum rough, with many large, whitish, rounded conspicuous papillae, arranged in 5 to 7 or 9 longitudinal rows on each neural annulus; dorsum yellowish-brown or unpigmented; **uncommon** but locally abundant in North America. (Fig. 12) *Helobdella papillata* (Moore 1906)
- 9a. Eyes in an approximately triangular pattern, the 1st pair always closer than the 2 posterior pairs (Fig. 2a) 10
- 9b. Eyes equidistant (Fig. 2b), in 2 paramedian rows; papillae in 6 longitudinal rows; with a pair of dark brown lines, interrupted by pale spots dorsally and ventrally, but the lines may be absent; body opaque; very common. (Fig. 13) *Glossiphonia complanata* (Linnaeus 1758)
- 10a. Body smooth; pigmentation slight, brownish-black in sparse clusters, and often with a dark median, longitudinal stripe (sometimes interrupted) on dorsum, but without paired lines; body translucent; **uncommon** in northern North America. (Fig. 14) *Glossiphonia heteroclita* (Linnaeus 1761)
- 10b. Body smooth; 4 to 7 mid-dorsal irregular, transverse bars, composed of brownish-black pigmentation; body translucent; North and South Carolina, **uncommon**. (Fig. 15) *Glossiphonia swampina* (Bosc 1802)



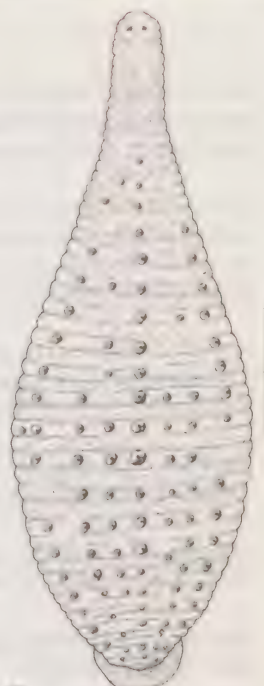
FIGS. 3-9. Leeches of freshwater mollusks. FIG. 3. *Marvinmeyeria lucida*. FIG. 4. *Helobdella stagnalis*. FIG. 5. *H. elongata*. FIG. 6. *H. transversa* (after Sawyer, 1972). FIG. 7. *H. fusca*. FIG. 8. *H. punctatolineata*. FIG. 9. *H. punctatolineata*. Scale lines = 2 mm.



10



11



12



13



14



15

FIGS. 10-15. Leeches of freshwater mollusks. FIG. 10. *Helobdella lineata*. FIG. 11. *H. lineata*. FIG. 12. *H. papillata*. FIG. 13. *Glossiphonia complanata*. FIG. 14. *G. heteroclita*. FIG. 15. *G. swampina*. Scale lines = 2 mm.

GLOSSARY

Annuli (sing. *Annulus*) - superficial segments of the somites. Basically there are 3 annuli per somite, each of which may be subdivided in some genera of leeches. Annulation can be most easily seen in the lateral margins of the middle region of the body.

Gonopores - external openings of the reproductive tracts, located on or in the furrow of the annulus on the ventral surface of somite XI and XII. The male gonopore is anterior to, larger than and more conspicuously visible than the female gonopore. In a few species the male and female ducts open into a common gonopore.

Neural Annulus - the annulus which contains the sensillae (segmental receptors). Since only 1 annulus of each somite contains sensillae, the neural annuli are a convenient outward indication of the true somite.

Papillae - protrusible sense organs scattered or in a series on the dorsal surface of the leech and thought to be tactile organs. (In some keys "tubercles" represent large papillae.)

Sensillae (segmental receptors) - whitish rounded metameric spots on neural annuli which contain cells that are though to be light-sensitive.

Somite - a true body segment or metamere. All leeches have 34 somites, each of which contains a nerve ganglion.

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CELLULAR INTERACTIONS IN THE EARLY DEVELOPMENT OF THE GASTROPOD EYE, AS DETERMINED BY DELETION EXPERIMENTS

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ABSTRACT

In *Bithynia* and *Lymnaea* the left eye is derived from micromere 1a and the right eye from 1c. Deletion of either of these cells results in the failure of the respective eye to develop, in the formation of a cephalic plate bridge ventral to the apical plate, and in a reduction in the number of apical plate cells. Deletion of 1b or 1d has no effect on eye development but affects the apical plate and cephalic plate in the same way as deletion of 1a or 1c. Eyes fail to develop in the absence of the vegetal cytoplasmic-inductive center at the critical period following the formation of the 3rd quartet of micromeres.

INTRODUCTION

Although the early students of molluscan cell lineage (see Raven, 1966) consistently showed that eyes developed from the cephalic plates (Verdonk, 1965) and the latter from the 1st quartet of micromeres, it was Clement (1967) who first gave conclusive evidence that the micromere 1a was most important in the origin of the left eye and 1c in the origin of the right eye. His deletion studies of the 1st quartet of micromeres alone would suggest a classic case of mosaic development, since deletion of 1a resulted in the absence of the left eye and deletion of 1c resulted in the absence of the right eye, while deletion of 1b or 1d had little or no effect. However, Clement pointed out that eyes had developed in D quarters (Clement, 1956) which lack the normal cells of origin, while lobeless embryos (Clement, 1952) and embryos with D, 1D or 2D removed (Clement, 1962) failed to develop eyes, even though 1a and 1c were present. Morrill, Blair & Larsen (1973) showed that half-embryos of *Lymnaea* could develop a normal pair of eyes and that normal eyes could develop in embryos after deletion of 2 or 3 of the 1st quartet micromeres. Verdonk & Cather (1973) found that CD-halves of *Bithynia* could develop paired or double eyes while both AD- and BC-2/4-embryos could develop eyes, even though lobeless embryos failed to do so (Cather & Verdonk, 1974).

As the complexity of the origin of the eyes became apparent, we felt it was necessary to do some comparison studies to determine whether or not there is a consistent developmental pattern, with similar controlling interactions, for the eyes of gastropods. Therefore, we decided to use the mesogastropod *Bithynia* and several species in the pulmonate family Lymnaeidae to repeat Clement's deletion studies on the neogastropod *Ilyanassa*.

MATERIALS AND METHODS

Lymnaea stagnalis, L. (*Stagnicola*) *palustris* and *Bithynia tentaculata* were collected from ditches near Utrecht, The Netherlands. *L. (Stagnicola) elodes* and *L. (S.) exilis* were collected from small ponds near Ann Arbor, Michigan, U. S. A. The snails were kept in the laboratory and egg masses were obtained from aquatic plants or aquarium walls after being spontaneously laid.

Cells were deleted from embryos within their capsules with a glass needle. In *Bithynia*, the D macromere can be identified by following the incorporation of the polar lobe into CD,

and then into D, which divides unequally to form 1d and 1D. With D specified, one can identify all the cells at the 8-cell stage. In the lymnaeids, as well as in *Bithynia*, the 1a and 1c micromeres meet broadly across the polar furrow at the animal pole, whereas 1b and 1d do not contact each other at the animal pole. Thus it is possible to distinguish 1a and 1c from 1b and 1d, but since other visible characteristics such as the polar lobe are absent, it is not possible to distinguish 1a from 1c or 1b from 1d in the lymnaeids.

The operated and control embryos were reared in relatively copper free tap water to an appropriate stage and fixed and stained with silver and studied as whole mounts. Details of all procedures are given by Morrill, Blair & Larsen (1973), Verdonk & Cather (1973) and Cather & Verdonk (1974).

RESULTS

Deletion of cells of the 1st quartet

Following deletion of individual micromeres of the 1st quartet, defects were detected only in the head region. Table 1 indicates the numbers of operations executed. Deletion of 1a always resulted in the loss of the left eye and tentacle (Fig. 11). Deletion of 1c always resulted in the loss of the right eye and tentacle (Fig. 12). Deletion of 1a or 1c, in those cases where it is not possible to distinguish between them, always resulted in the loss of 1 eye and the adjacent tentacle (Figs. 2, 3, 4). In those cases where an analysis of the cell pattern could be done, there was a reduction in the number of cells in the apical plate, and an antero-ventral bridge of cephalic plate cells was uniformly present below the apical plate (Figs. 3, 4, 8). In 18 -1a or -1c embryos analyzed, 11 had 4 cells in the apical plate, 5 had 5 cells, and 2 had 3 cells. All embryos lacking a left eye had 4 apical plate cells except 1. Of those lacking the right eye, 5 had 5 cells, 2 had 4 cells, and 2 had 3 cells (Fig. 4).

TABLE 1. Number of embryos examined following deletion of 1st quartet micromeres.

Species	Micromeres deleted			
	-1a	-1b	-1c	-1d
<i>Bithynia</i>	7	3	5	2
	-1a or 1c	-1b or 1d	-1m	
<i>Bithynia</i>	4	9	6	
<i>Lymnaea stagnalis</i>	3	4	1	
<i>L. (Stagnicola) palustris</i>	8	7	9	
<i>L. (S.) exilis</i>	3	4	-	

Deletion of 1b or 1d in *Bithynia* results in the development of an embryo of normal appearance. There are slight differences in the cell pattern of the head, but the large number of cells in the head region and the absence of a cell lineage make a detailed analysis extremely difficult. Defects in the head cell pattern, such as is seen in *Lymnaea*¹, will almost certainly be found when the cell lineage of operated and control embryos can be compared. Deletion of 1b or 1d in the lymnaeids allows

¹Since all lymnaeid embryos appeared identical in our experiments, statements below referring to *Lymnaea* also apply to *Stagnicola*.

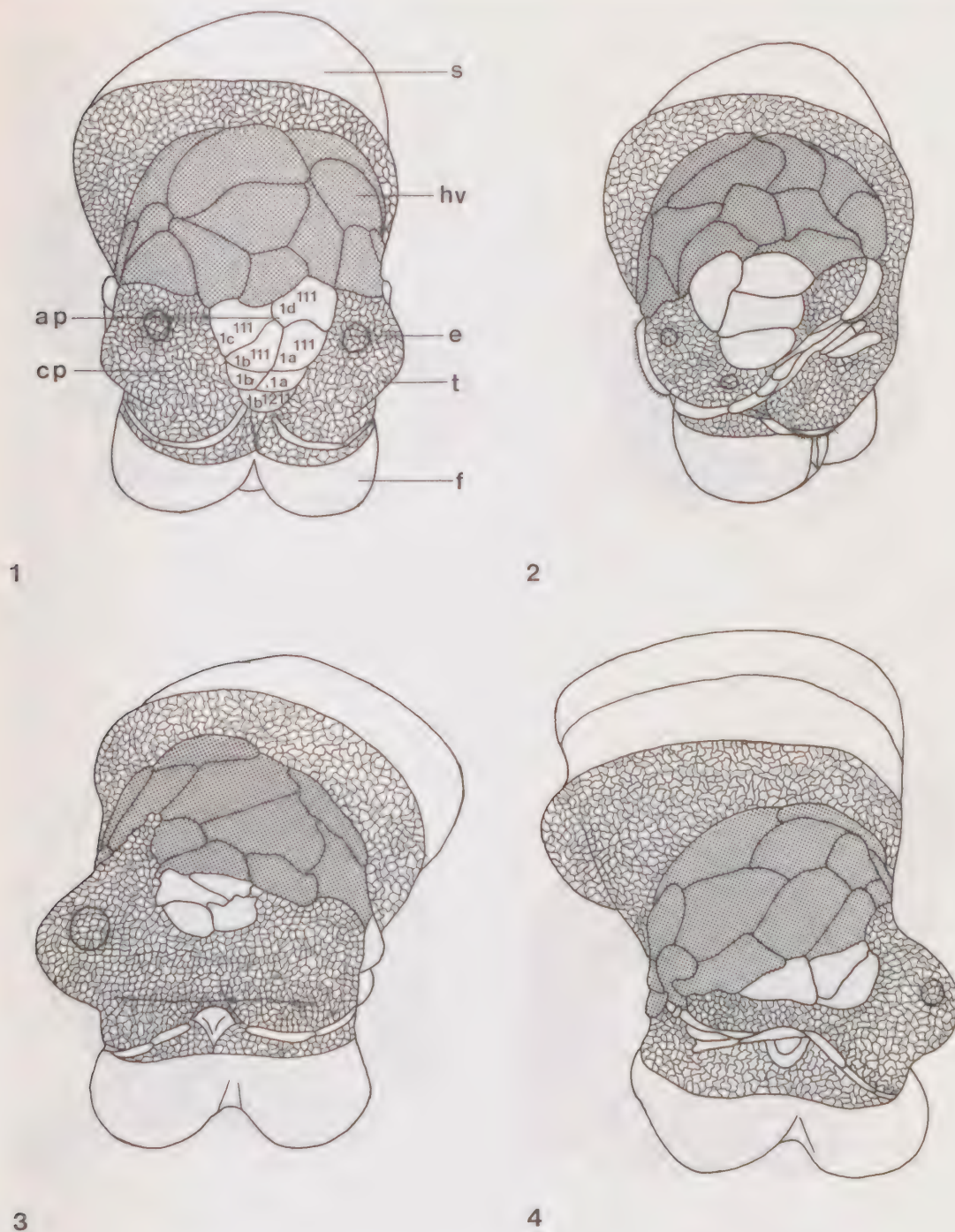


FIG. 1. Control embryo of *Lymnaca (Stagnicola) palustris*. The apical plate cells (ap) are clear and designated by their quadrant of origin. The cephalic plates (cp) are made of small cells which give rise to the eyes (e) and tentacles (t). The head vesicle cells (hv) are stippled. The foot (f) and shell (s) are shown for orientation. The same patterns are used throughout the remaining figures to designate the respective areas. FIG. 2. Embryo of *L. stagnalis* following deletion of 1a or 1c. FIG. 3. Embryo of *L. (S.) palustris* following deletion of 1a or 1c. FIG. 4. Embryo of *L. (S.) palustris* following deletion of 1a or 1c.

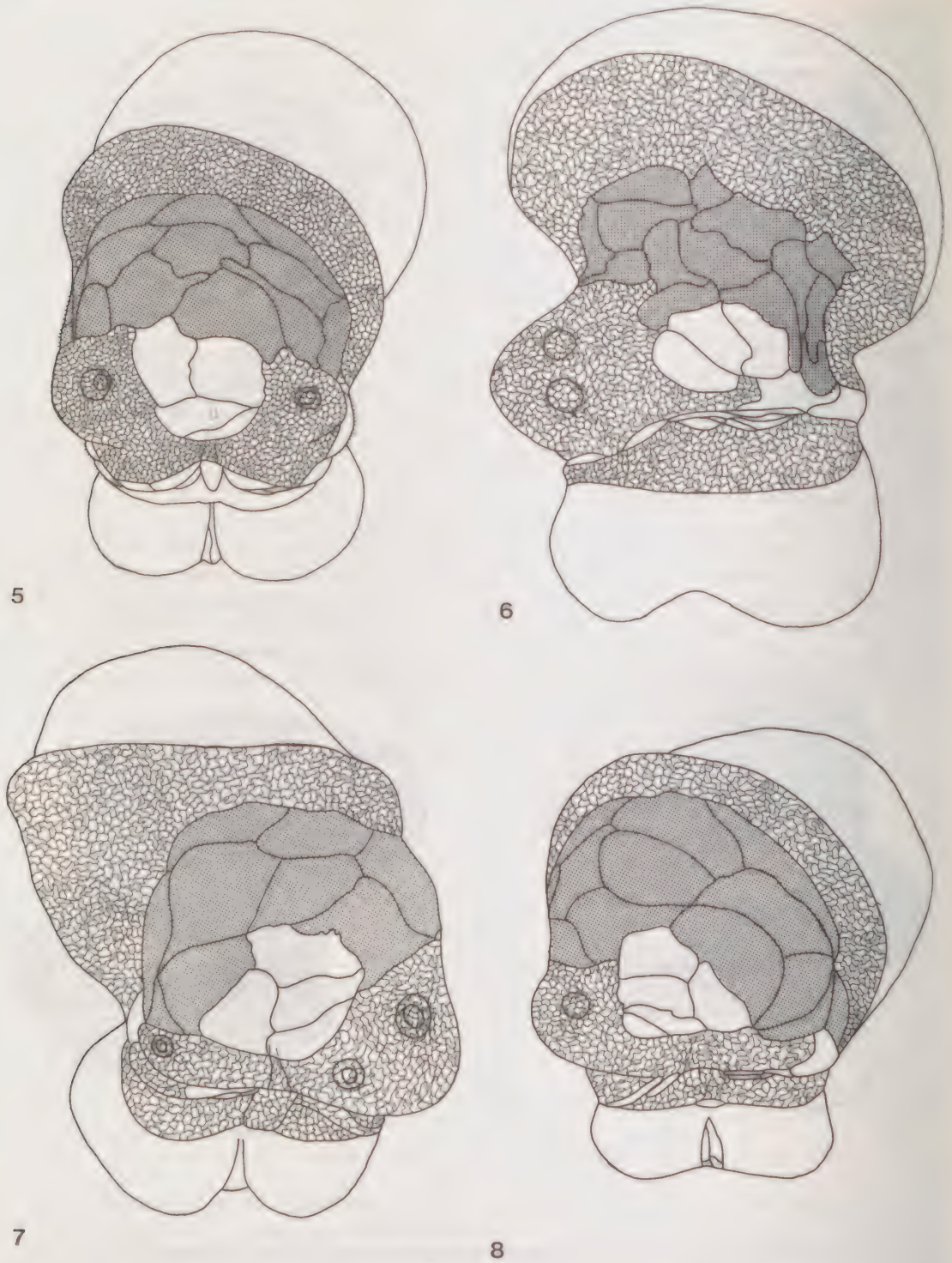
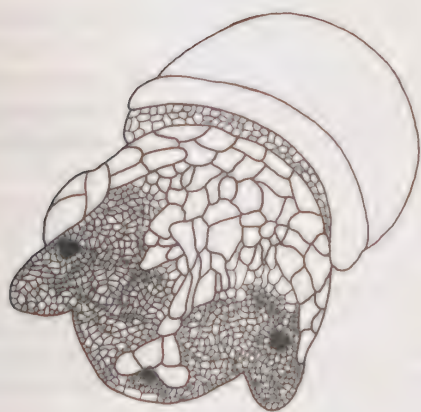


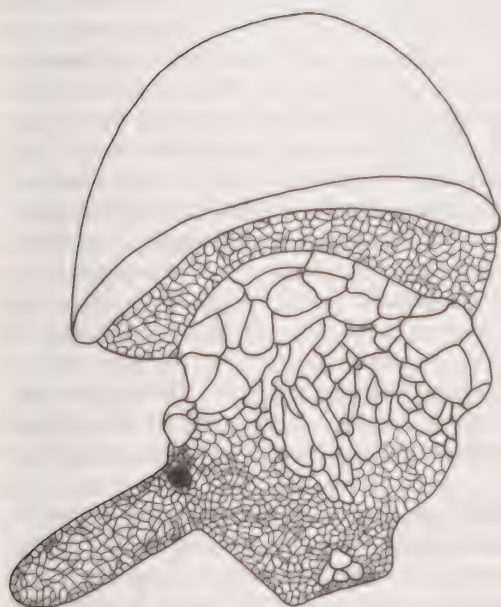
FIG. 5. Embryo of *Lymnaea stagnalis* following deletion of 1b or 1d. FIG. 6. Embryo of *L. stagnalis* following deletion of an unknown 1st quartet micromere. FIG. 7. Embryo of *L. stagnalis* following deletion of 1b or 1d. FIG. 8. Embryo of *L. stagnalis* following deletion of 1a or 1c.



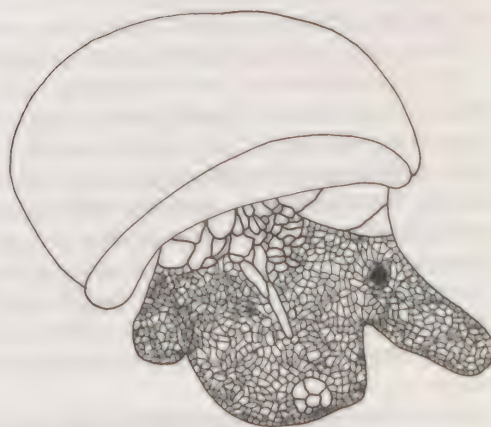
9



10



11



12

FIG. 9. Control embryo of *Bithynia tentaculata*. FIG. 10. Embryo of *B. tentaculata* following deletion of 1d. FIG. 11. Embryo of *B. tentaculata* following deletion of 1a. FIG. 12. Embryo of *B. tentaculata* following deletion of 1c.

development of a snail embryo which superficially appeared normal, but analysis of the cell pattern (Figs. 5, 7) revealed that the number of cells in the apical plate is reduced (compare to control, Fig. 1). Of 24 -1b or -1d embryos, 15 had 4 apical plate cells, 7 had 5, and 2 had 3.

The most common additional defect following deletion of any 1st quartet micromeres was doubling of the eye on one side of the embryo (Figs. 2, 6, 7). This occurred in 6 of 56 embryos considered.

In one case in *Bithynia*, following deletion of an unknown 1st quartet micromere (-1m), a single median eye developed with a left tentacle. Otherwise, the operated embryos were free of observed defects and development following each type of operation was consistent within the group.

DISCUSSION

The results of deletion of individual micromeres of the 1st quartet from embryos of *Bithynia* and *Lymnaea* are consistent with those of Clement (1967) and support the cell lineage studies of Verdonk (1965). Deletion of 1a involves the loss of the left eye and tentacle, and deletion of 1c involves the loss of the right eye and tentacle.

Even though it has been clearly shown that 1b and 1d contribute to the cephalic plates in *Lymnaea* (Verdonk, 1965) and *Biomphalaria* (Camey & Verdonk, 1970), and that it is from the cephalic plates that the eyes and tentacles develop, these cells' contributions are not critical in the development of the eyes or tentacles in either *Ilyanassa* or in the species that we have studied. With existing information, it is not possible to determine if 1b or 1d contribute significantly to other cephalic plate structures in these species or whether regulation occurs so that any contribution that these cells might normally make to the eye is taken over by progeny of 1a or 1c. Clement (1967) found that deletion of 1b most often resulted in synopthalmia, but that no effect on the development of the right eye was observed.

We have observed no obvious synopthalmia after deletion of 1b, but we suggest that in -1b or -1d operations, embryos that have only 3 or 4 cells in the apical plate are -1b and those with 5 cells are -1d. Normally 1b contributes 3 of the 7 cells to the apical plate while 1d contributes only 1. The absence of synopthalmia may be due to the fact that the ventral bridge of cephalic plate cells, seen after all the types of operations reported here, have maintained a more or less normal spatial relation between the eye-forming areas of the cephalic plates. In synopthalmic embryos of *Lymnaea* produced by LiCl treatment (Verdonk, 1965, 1968), the cephalic plates formed bridges dorsal to the apical plate. A 3rd eye in the dorsal bridge was not uncommon and cyclopia occurred when the bridge was particularly large.

In a classic mosaic system, one would expect the number of cells present to be the same as in the control except for those derived from the deleted cell. In the apical plate this is generally not the case. There are usually fewer cells than can be accounted for by simple deletion. For instance, embryos attributed to deletion of 1d would be expected to have 6 cells in the apical plate, but never more than 5 were observed. Verdonk (1965) showed that changes in the division axis of the basal cell of the dorsal arm of the cross were correlated with the release of inhibition of cell division so that instead of producing 2 normally large head vesicle cells, division would continue to form many small cells which would contribute to the dorsal bridge of cephalic plate cells. The loss of apical plate cells not accounted for by a deletion is probably the result of changes in the orientation of the remaining cells which must fill the space caused by the deletion. With the change

in orientation, the inhibition to divide is lost and presumptive apical plate cells become small cephalic plate cells and form the ventral bridge.

In normal development the cells $1b^{12121}$ and $1b^{12122}$ form the ventral parts of the cephalic plates. The derivatives of $1b^{12121}$ shift to the right cephalic plate and those of $1b^{12122}$ to the left cephalic plate (see Verdonk, 1965, figs. 21 and 22). If this displacement does not occur, a ventral bridge, which connects the cephalic plates from the left and right sides, is formed (see Verdonk & de Groot, 1970: 182). Apparently for the shifting of the future cephalic plate cells, originating from the b-arm of the cross, a normal apical plate is essential. If the apical plate consists of a smaller number of cells than a normal plate, the derivatives of $1b^{12121}$ and $1b^{12122}$ stay connected and form a ventral bridge, even when most of the corresponding cephalic plate is missing for the deletion of 1a or 1c (Figs. 2, 3, 4, 8). After deletion of 1b the ventral part of the apical plate is missing. Now the left and right cephalic plate may fuse ventrally, and in this way an embryo as shown in Fig. 7 may originate. As 1d gives an unimportant contribution to the cephalic plates, these structures have to be nearly normal in -1d embryos. An embryo with 2 cephalic plates, each with an eye, may originate as shown in Fig. 5, which most probably is a -1d embryo. Typically, as in this embryo, the apical plate is smaller than normal and a ventral bridge is present.

So far the discussion would lead one to view the development of gastropod eyes as a rather rigidly fixed cell limited system. Clement (1967) has already shown that this is not the case in *Ilyanassa*. He has shown that the formation of the eyes is dependent on the vegetal cytoplasm present in the polar lobe and distributed to the D macromeres. The influence of this special cytoplasm is exerted during a specific period between the formation of the 3rd quartet of micromeres and the formation of the mesentoblast.

Morrill, Blair & Larsen (1973) described normal eyes in half embryos of *Lymnaea* as well as in those with 2 or 3 of the 1st quartet micromeres deleted. They attribute these results to the ability of the cells to organize themselves around the D quadrant macromere by the critical inductive period.

Raven (1952, 1966, 1968, 1974) and Raven, Bezem & Baretta-Bekker (1973) have studied this period intensively in *Lymnaea* and have shown that the inductive center lies in 3D and that ectosomes apparently break up and pass RNA into the adjacent micromeres. Contact between the micromeres and the 3D macromere is required at this stage for the establishment of bilateral symmetry (Verdonk, 1968). The absence of synophthalmia or cyclopia in our operated embryos may be due to the distribution of cephalic plate cells below the presumptive apical plate cells so that they are out of position to receive the eye forming stimulus at the critical period. The dorsal bridges of cephalic plate cells produced after LiCl exposure are well situated for the inductive interaction.

Verdonk & Cather (1973) have shown that the interactions normally restricted to the D quadrant in most molluscs are shared with C in *Bithynia*. This is attributed to a precocious breakdown of the vegetal body so that C as well as D receive its products. It is interesting that all aspects of eye development in *Bithynia* are similar to the other species even though there is greater variability in the inductive system.

It thus appears that the early development of the gastropod eye involves a complex sequence of events, with an early temporary fixation of the ectodermal cells derived from 1a and 1c. These cells then require an inductive stimulus from the vegetal cytoplasm. The absence of the specific ectodermal cell which will normally form the eye evidently does not feed back adequate information so that other ectodermal cells will form eyes. However, loss of 1/2 or 3/4 of the embryo which

includes the presumptive eye cells is recognized, and other ectoderm then responds to the inductive influence to form eyes.

There is much yet to be learned about the interactions which lead to the formation of the gastropod eye, which has heretofore been viewed as a simple system.

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REPARTITION LOCALE ET BIOGEOGRAPHIE DES MOLLUSQUES DULÇAQUICOLES DE LA GUADELOUPE (ANTILLES FRANÇAISES)¹

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RESUME

La répartition des 21 espèces qui composent la faune malacologique dulçaquicole de la Guadeloupe a été étudiée. Trois principaux groupes d'espèces ont été distingués: espèces d'eau courante, espèces d'eau stagnante et espèces vivant indifféremment dans les 2 sortes de milieux. Les 3 espèces les plus courantes sont *Biomphalaria glabrata*, Mollusque vecteur de la Bilharziose, *Ampullaria glauca* et *Physa marmorata*. Une comparaison des gîtes de ces 3 espèces montre que *B. glabrata* et *P. marmorata* se tolèrent parfaitement dans de nombreux biotopes. Par contre, le phénomène d'exclusion partielle qui semble exister entre *B. glabrata* et *A. glauca* est peut être le fait de la préférence de cette dernière espèce pour les milieux courants.

Aucun Mollusque d'eau douce n'est endémique à la Guadeloupe et la plupart des espèces ont une extension très large dans l'hémisphère nord et également dans l'hémisphère sud où on y retrouve 13 des 21 espèces de la faune malacologique guadeloupéenne.

INTRODUCTION

Les études malacologiques qui ont été menées en Guadeloupe au cours des années 1972-1973 ont permis d'établir un catalogue détaillé des espèces dulçaquicoles (Pointier, 1974). La prospection était essentiellement axée sur la recherche de *Biomphalaria glabrata*, qui est la principale espèce vectrice de la bilharziose dans les Antilles et en Amérique du Sud. Au Brésil, cependant, *B. straminea* (commun aussi sous le nom d'*Australorbis centimetralis*) est un mollusque vecteur également important et qui serait en extension (Pan. Amer. Hlth. Org., 1968). Deux autres espèces présentes dans les mêmes régions sont également susceptibles d'infestation par *Schistosoma mansoni*: *B. peregrina* et *B. havanensis* (Richards, 1963; Barbosa, Barbosa & Rodriguez, 1958). Les 3 espèces, *straminea*, *peregrina* et *havanensis*, sont très voisines et peuvent prêter à confusion bien que de nombreuses études anatomiques aient été réalisées par des auteurs brésiliens (Paraense, 1963, 1966; Paraense & Deslandes, 1955a, 1955b, 1958). En Guadeloupe, le problème est plus simple: les études anatomiques et les tests d'infestation ont montré qu'il n'y avait qu'une seule espèce vectrice de la Bilharziose, *B. glabrata*.

¹ Etudes réalisées dans le cadre d'un contrat de la Délégation Générale à la Recherche Scientifique et Technique, Mollusques vecteurs, Lutte biologique, convention 727 0165 Coordinateur Pr. Y.J. Golvan. La récolte du matériel malacologique a été réalisée en collaboration avec les chercheurs et techniciens des laboratoires participant à l'action concertée: Laboratoire de parasitologie, Faculté de médecine Saint-Antoine, 27 rue de Chaligny, Paris - Laboratoire de parasitologie, Faculté de médecine de Créteil, 6 rue du Général Sarrail, Créteil - Département de biologie animale, Collège scientifique universitaire de Perpignan, Avenue de Villeneuve, Perpignan - Laboratoire de Biologie marine et Malacologie, Ecole Pratique des Hautes Etudes, 55 rue Buffon, Paris - Ecole Nationale Vétérinaire de Lyon, 2 Quai Chauveau, Lyon.

Par ailleurs, 20 autres espèces de Mollusques sont présentes dans les eaux douces guadeloupéennes.

REPARTITION ET DENSITE DES ESPECES EN GUADELOUPE

La Guadeloupe est un système insulaire comprenant 2 îles principales: la Grande Terre (585 km²) formée d'une série de plateaux calcaires d'origine corallienne et la Basse Terre ou Guadeloupe proprement dite (848 km²), qui est une île montagneuse volcanique. Les autres îles les plus importantes qui complètent l'archipel sont la Désirade, Marie Galante et les Saintes. Les 2 îles principales offrent une grande diversité de biotopes. La Basse Terre, très arrosée, est le domaine des eaux courantes: torrents de montagne, rivières et nombreux canaux. En Grande Terre, au contraire, les biotopes sont constitués par des eaux stagnantes, mares, marécages, et également par quelques ravines temporaires.

Dans le Tableau 1, nous avons fait le bilan du nombre de stations où chaque espèce de Mollusque a été récoltée. Les stations ont été divisées en plusieurs catégories: rivières, canaux, mares, marécages. A ces 4 types de biotopes, nous avons ajouté les mangroves lacustres, les micro-biotopes que constituent les infiltrations d'eau le long des rivières, canaux, etc., et les bassins ou autres réservoirs qu'on trouve dans de nombreuses distilleries abandonnées et qui sont en fait des petites mares artificielles.

Toutes ces stations ont été regroupées en 2 grandes catégories: les milieux "courants" et les milieux "stagnants." Ces 2 groupes principaux ne tiennent pas compte des gîtes dits "d'infiltrations" qui peuvent être considérés comme des milieux intermédiaires, stagnants à certaines périodes, courants à d'autres, et dépendant surtout des conditions microclimatiques existantes. L'examen des chiffres du Tableau 1 nous permet de classer la faune malacologique de Guadeloupe en 3 groupes principaux: (1) Les espèces d'eau courante: *Potamopyrgus coronatus*, *Physa cubensis*, *Neritina virginea*, *N. punctulata*, *N. succinea* et *Helisoma foveale*; (2) Les espèces d'eau stagnante: *Drepanotrema lucidum*, *D. kermatoides*, *D. aeruginosum*, *D. analinum*, *D. cimex*, *Biomphalaria schrammi*, *Eupera viridans*, *Pleisiophysa granulata*, *Lymnaea cubensis* et *Dreissena* sp.; (3) Les espèces ubiquistes qui habitent indifféremment les 2 types de milieux: *Physa marmorata*, *Biomphalaria glabrata*, *Gundlachia radiata*, *Ampullaria glauca* et *Pisidium punctiferum*. Les 2 dernières espèces ayant cependant une certaine préférence pour les eaux courantes.

Trois Mollusques paraissent donc dominer la faune malacologique de Guadeloupe: *Biomphalaria glabrata*, *Physa marmorata* et *Ampullaria glauca*. Ces 3 espèces sont en effet capables de s'adapter à des biotopes très divers. Cependant, il convient de rappeler que l'effort de prospection avait porté essentiellement sur les gîtes à Planorbes et que certaines espèces ont probablement été négligées, comme les Néritines qui sont présentes dans la plupart des très nombreux torrents de Guadeloupe. Quoi qu'il en soit, *B. glabrata*, *P. marmorata* et *A. glauca*, qui sont des espèces ubiquistes, sont certainement les plus communes de l'île.

Certains auteurs ont mis en évidence, pour l'Afrique et la zone néotropicale, des possibilités de lutte biologique contre les planorbes vecteurs de la bilharziose par introduction d'autres Mollusques qui seraient des compétiteurs ou des prédateurs. Ainsi, Verdcourt (1971) indique que *Physa acuta* serait nuisible aux cultures de *Biomphalaria* africains, et à Porto Rico, *Marisa cornuarietis* (Ampullariidae) a été utilisé dans des essais de lutte biologique contre *B. glabrata* (Ruiz-Tiben, Palmer & Ferguson, 1969; Jobin & Berrios-Duran, 1970; Jobin, Ferguson & Berrios-Duran, 1973). Il était donc intéressant pour la Guadeloupe, de comparer les répartitions de *B. glabrata*, Mollusque vecteur, avec les représentants locaux de la

TABEAU 1. Répartition de la faune malacologique dulçaquicole en Guadeloupe.

Espèces	Biotores										
	Milieux courants					Gites d'infiltrations	Milieux stagnants				
	Ruisseaux Rivières Ravines	Canaux	# stations eaux courantes (Total)	Bassins et réservoirs	Mangrove lacustre		Mares et étangs	Marécages Prairies inondées	# stations eaux stagnantes (Total)	Total général des stations étudiées	
<i>Biomphalaria glabrata</i>	13	38	51	9	10	1	58	5	74	134	
<i>Physa marmorata</i>	22	33	55	18	7	1	41	5	54	127	
<i>Ampullaria glauca</i>	31	42	73	4	4	1	24	1	30	107	
<i>Drepanotrema lucidum</i>	2	1	3			1	43	1	45	48	
<i>Drepanotrema kermatoides</i>	2	1	3	1		1	34	3	38	42	
<i>Potamopyrgus coronatus</i>	17	9	26		1		4	3	8	34	
<i>Gundlachia radiata</i>	5	7	12	2		1	7		8	22	
<i>Eupera viridans</i>	2		2			1	15		16	18	
<i>Biomphalaria schrammi</i>	2	1	3			1	12		12	15	
<i>Neritina punctulata</i>	10	2	12							12	
<i>Neritina virginea</i>	8	2	10					1	1	11	
<i>Pleisiophrysa granulata</i>							7	2	7	7	
<i>Pisidium punctiferum</i>		5	5				3	2	5	5	
<i>Lymnaea cubensis</i>										5	
<i>Physa cubensis</i>	1	4	5							4	
<i>Neritina succinea</i>	4		4					3	4	4	
<i>Drepanotrema aeruginosum</i>								2	4	4	
<i>Drepanotrema anatinum</i>						1	2	1	2	2	
<i>Dreissena</i> sp.									1	1	
<i>Drepanotrema cimex</i>										1	
<i>Helisoma foveale</i>	1		1							1	

famille des Ampullariidae et des Physidae. L'inventaire et le recoupement des résultats concernant les 3 espèces, *B. glabrata*, *Ampullaria glauca* et *P. marmorata*, est le suivant:

Groupe *Biomphalaria glabrata* - *Ampullaria glauca*

Sur un total de 208 stations où nous avons récolté les 2 Mollusques, 37 seulement hébergent les 2 espèces en même temps, alors que 96 hébergent *Biomphalaria glabrata* seul (ou avec d'autres espèces que *Ampullaria glauca*) et 75, *A. glauca* seul (ou avec d'autres espèces que *B. glabrata*). Il n'y a donc que 17.7% des stations prospectées qui hébergent les 2 espèces ensemble. *A. glauca*, au vu des résultats exposés précédemment, semble avoir une préférence pour les milieux courants (70.8% ont été récoltés dans les milieux courants contre 29.2% dans les milieux stagnants), alors que *B. glabrata* lui, est plus tolérant (40.8% dans les milieux courants contre 59.2% dans les milieux stagnants). Ces résultats pourraient expliquer ce phénomène d'exclusion partielle qui est observé, *B. glabrata* ayant une légère préférence pour les milieux stagnants et *A. glauca* pour les milieux courants. Quoi qu'il en soit, dans les milieux fermés qui seraient les plus propices à une compétition entre espèces, *A. glauca* et *B. glabrata* semblent se tolérer parfaitement. Si l'on considère les 37 stations communes aux 2 espèces, on constate que 15 sont constituées par des eaux stagnantes et 22 par des eaux courantes. Ces résultats sont assez représentatifs des gîtes des 2 espèces.

Groupe *Biomphalaria glabrata* - *Physa marmorata*

Ces 2 espèces apparaissent beaucoup plus proches que les précédentes puisque cette fois-ci, sur 182 stations, près de la moitié (44.1%) héberge les 2 espèces en même temps alors que 29.6% hébergent *Biomphalaria glabrata* seul et 26.3% *Physa marmorata* seul. Ces résultats paraissent logiques puisque *P. marmorata* n'a pas de préférence marquée pour l'une ou l'autre catégorie de milieux. Par ailleurs, les gîtes communs aux 2 espèces sont également répartis de la même manière: 44.6% de milieux courants pour 55.4% de milieux stagnants. *B. glabrata* et *P. marmorata* sont donc 2 espèces qui se tolèrent parfaitement dans la nature en Guadeloupe.

REPARTITION GEOGRAPHIQUE DE LA FAUNE MALACOLOGIQUE GUADELOUPEENNE

Biomphalaria glabrata

Un grand nombre de noms de genres et d'espèces ont été attribués à *Biomphalaria glabrata* un peu partout dans la zone néotropicale. Paraense (1961) considère 11 espèces comme synonymes d'*Australorbis glabratus*, et Harry (1962) dresse un catalogue des noms de genres et d'espèces de Planorbidae dans lequel il groupe 23 espèces sous la dénomination de *Taphius glabratus*. Les synonymes qui paraissent les plus valides ont été signalés dans les Antilles et en Amérique du Sud:

Planorbis glabratus a été décrit pour la première fois par Say en 1818 comme provenant de la Caroline du Sud. Cependant, ce planorbe n'a jamais été retrouvé depuis dans cette localité, et Pilsbry (1934) a montré que les coquilles décrites par Say provenaient en fait de la Guadeloupe et donc correspondaient au *Planorbis guadeloupensis* que Sowerby avait décrit en 1822. La dénomination *glabratus* prévaut donc sur celle de *guadeloupensis*.

Wagner, en 1827, publie un catalogue des coquilles qui ont été récoltées par Spix au cours d'un voyage au Brésil en 1817-1820. Parmi celles-ci, nous citerons les 6 espèces qui ont été trouvées dans la région de Bahia et qui sont considérées comme des synonymes de *Biomphalaria glabrata*: *Planorbis olivaceus* Spix, *P. ferrugineus* Spix, *P. lugubris* Wagner, *P. nigricans* Spix, *P. albescens* Spix et *P. viridis* Spix.

En 1838, 2 espèces sont signalées par Beck dans l'index Molluscorum: *Planorbis antillarum* Beck dont l'origine est peu précise (Antilles) et *P. lundii* Beck, qui a été placé en synonymie avec *P. olivaceus* par Germain (1921). Beck signale ce planorbe au Brésil.

Anton (1839) décrit *Planorbis concavospira* également d'origine peu précise (Amérique du Sud) et, en 1853, Moricand cite un *P. dentifer* originaire de Bahia.

En 1859, Drouët trouve en Guyane française et au Surinam *Planorbis xerampelinus* et, en 1878, Sowerby publie la description d'un planorbe de l'île d'Antigue qu'il nomme *P. antiguensis*.

Dans *Systematisches Conchylien-Cabinet* de Martini & Chemnitz, vol. 1(17), 1886, plusieurs espèces sont décrites par Dunker: *Planorbis bahiensis* de Bahia, *P. becki* du Brésil également et *P. bolivianus* de Bolivie.

En 1921, Germain fait une révision des Mollusques de l'Indian Museum de Calcutta et cite *Planorbis blauneri* Shuttleworth en provenance de l'île de Vieques (près de Porto Rico).

Lutz (1923) publie la description de *Planorbis immunis* de Rio de Janeiro, et Pilsbry (1934) donne celle de la variété *Australorbis glabratus christophorensis* de l'île de Saint Kitts.

Toutes ces espèces ont donc été considérées comme des synonymes probables de *Biomphalaria glabrata* par Paraense (1961) et Harry (1962). La limite nord de répartition de l'espèce semble donc être Haiti et la limite sud, l'état de Parana au Brésil (voir cartes).

Dans l'hémisphère nord, on trouve *Biomphalaria glabrata* dans un certain nombre d'îles antillaises: Haiti (Crosse, 1892; Paraense & Corrêa, 1963), Saint Domingue (Crosse, 1891, 1892), Porto Rico (Crosse, 1892; Ferguson & Richards, 1963; Harry & Hubendick, 1964), Vieques (Germain, 1921), Saint Martin (Coomans, 1967), Saint Kitts (Pilsbry, 1934), Antigua (Sowerby, 1878), Montserrat (Pointier, 1975a), Guadeloupe (Schramm, 1869; Mazé, 1883; Crosse, 1892; Grétilat, 1967; Floch, 1969; Pointier, 1974), Dominique,² Martinique (Mazé, 1874; Dreyfuss, 1953; Grétilat, 1967) et Sainte Lucie (Sturrock, 1975). *B. glabrata* serait également présent à Curaçao (Kuyp, 1949, 1951), au Vénézuéla (Vernhout, 1914; Baker, 1930) et dans les Guyanes (Vernhout, 1914).

Dans l'hémisphère sud, *Biomphalaria glabrata* a été récolté au Brésil (Wagner, 1827; Haas, 1939; Morretes, 1945; Lucena, 1956; Paraense & Corrêa, 1963).

Biomphalaria glabrata serait donc absent au nord de Haiti. Pourtant, la faune malacologique de Cuba a été bien étudiée (Aguayo & Jaume, 1947), et l'île héberge plusieurs espèces de *Biomphalaria* et de *Drepanotrema* dont les exigences écologiques sont assez voisines de celles de *B. glabrata* (*B. havanensis*, *D. lucidum*, *D. kermatoides*...). La faune du sud des U.S.A. (Floride, Texas, Louisiane, Caroline du sud...) est également bien connue. Dans les Petites Antilles, beaucoup d'îles hébergent *B. glabrata* et la répartition est à peu près égale entre les îles

²Communication orale à la 6ème réunion annuelle du Comité Caraïbe pour la lutte contre la bilharziose - Caravelle le 26 et 27 avril 1973 - L'introduction de *Biomphalaria glabrata* en Dominique serait récente.



FIG. 1. Carte de répartition de *Biomphalaria glabrata* dans les Antilles et en Amérique du Sud. 1, Hispaniola (Haïti et Saint Domingue); 2, Porto Rico; 3, Vieques; 4, Saint Martin; 5, Saint Kitts; 6, Montserrat; 7, Antigua; 8, Désirade; 9, Marie Galante; 10, Guadeloupe; 11, Dominique; 12, Martinique; 13, Sainte Lucie; 14, Curaçao; 15, Vénézuéla; 16, Guyanes (Guyane française et Surinam); 17, Brésil (Parà); 18, Brésil (Maranhão); 19, Brésil (Rio Grande do Norte); 20, Brésil (Parahiba); 21, Brésil (Pernambucco); 22, Brésil (Alagoas); 23, Brésil (Bahia); 24, Brésil (Goiás); 25, Brésil (Minas Gerais); 26, Brésil (Espírito Santo); 27, Brésil (Rio de Janeiro); 28, Brésil (Paràna).

basses et calcaires (Marie Galante, Désirade, Grande Terre, Antigua, Saint Martin), et les fles Hautes à volcanisme encore actif (Sainte Lucie, Martinique, Dominique, Guadeloupe, Montserrat). Sur le continent sud-américain, *B. glabrata* est présent à l'est des Andes et paraît essentiellement répandu dans les zones de forte concentration humaine, c'est-à-dire, principalement, au nord du Vénézuéla, des

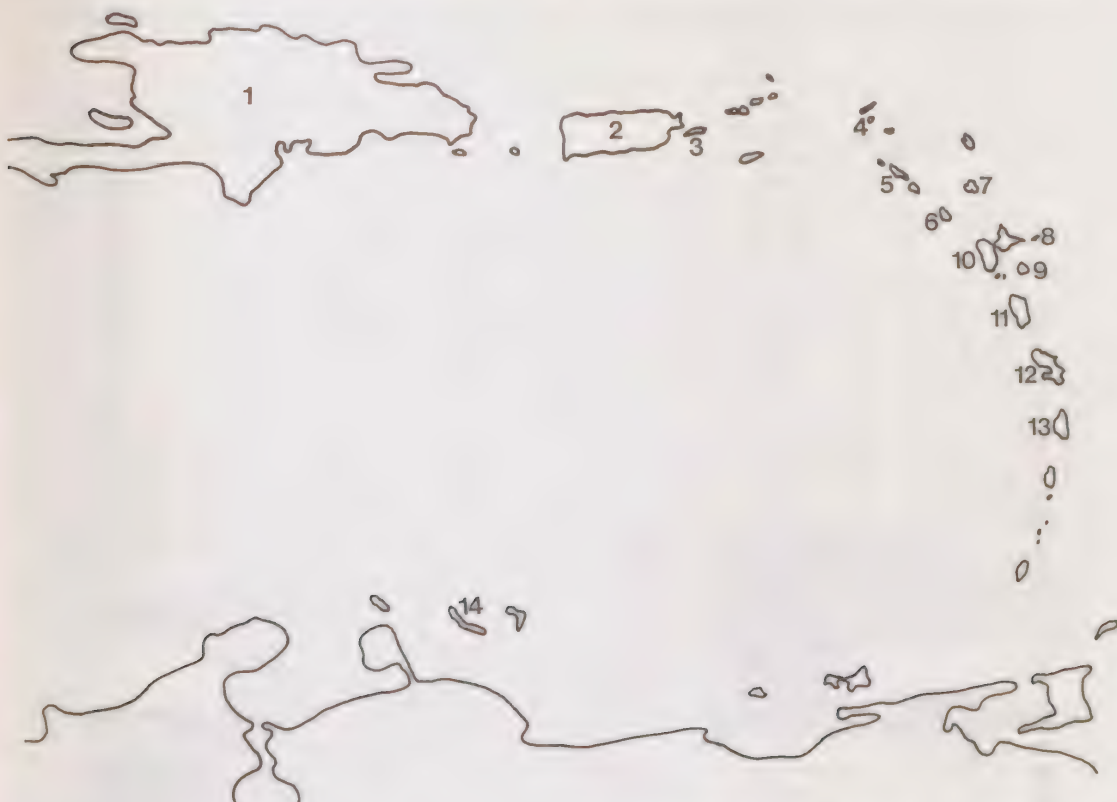


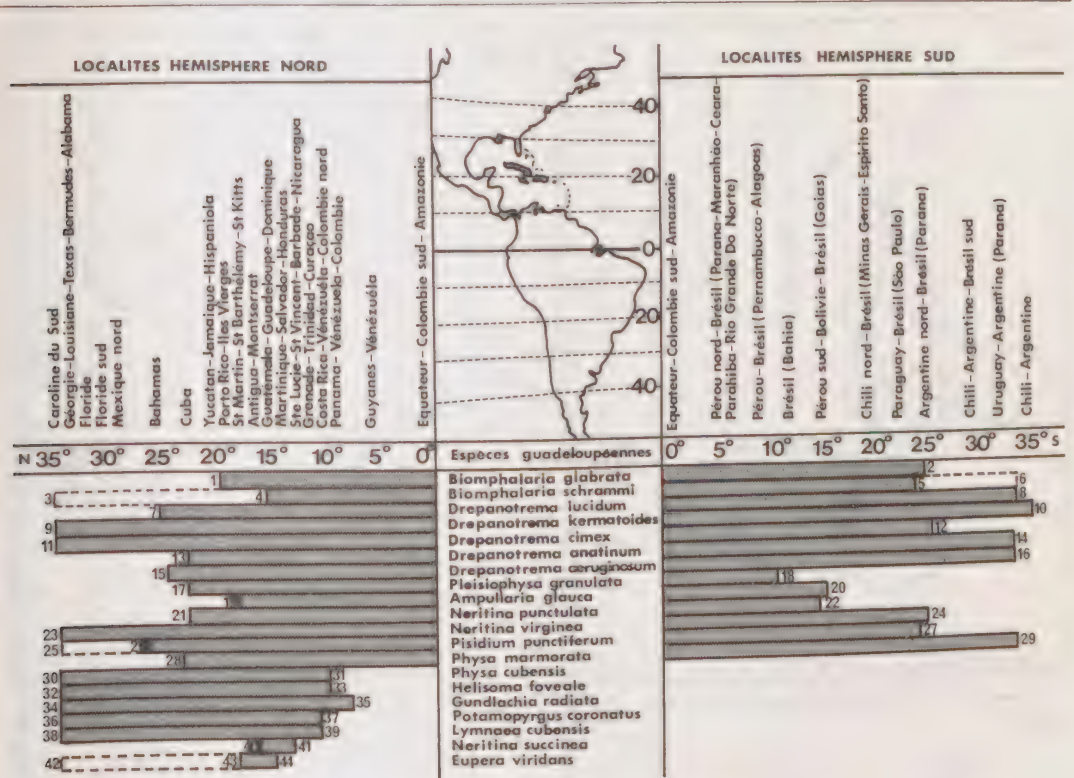
FIG. 2. Carte de répartition de *Biomphalaria glabrata* dans les Antilles. 1, Hispaniola (Haïti et Saint Domingue); 2, Porto Rico; 3, Vieques; 4, Saint Martin; 5, Saint Kitts; 6, Montserrat; 7, Antigua; 8, Désirade; 9, Marie Galante; 10, Guadeloupe; 11, Dominique; 12, Martinique; 13, Sainte Lucie; 14, Curaçao.

Guyanes et, après une interruption pour la zone amazonienne, au Brésil, dans les états côtiers de Rio Grande do Norte, Parahiba, Pernambuco, Alagoas, Bahia, Espirito Santo, Rio de Janeiro, etc. La limite sud de l'extension de l'espèce se situe dans l'état de Parana (voir Tableau 1 et carte). En Bolivie, la seule référence fournie par la littérature est la description de *Planorbis bolivianus* par Dunker, espèce qui fut considérée par la suite comme un synonyme de *B. glabrata* (Harry, 1962). Elle ne semble pas avoir été récoltée depuis. En 1914, Vernhout, dans son tableau de répartition des espèces, a signalé la présence de *P. guadeloupensis* en Colombie ainsi que celle de *P. olivaceus* au Mexique. Plus récemment, Harry & Hubendick (1964) ont exclu de ces régions la présence de *B. glabrata*. Vernhout ne cite pas les sources de ses 2 renseignements qui, à défaut de confirmation, seront donc considérés comme douteux. Par ailleurs, *B. glabrata* n'a jamais été signalé en Amérique centrale.

Les autres espèces de la faune guadeloupéenne

Le Tableau 2 fait le bilan de la distribution géographique générale des 21 espèces guadeloupéennes. Beaucoup de références ont été empruntées à la littérature du XIX^{ème} siècle et, de ce fait, doivent être considérées avec une certaine prudence. En effet, d'une part, des espèces ont pu disparaître de diverses localités, et d'autre

TABLEAU 3. Aires de répartition des espèces guadeloupéennes dans les hémisphères nord et sud.*



* Les numéros des histogrammes correspondent aux localités suivantes: 1, Hispaniola (Crosse, 1891); 2, Brésil (Parana) (Lucena, 1956); 3, Louisiane, Texas (Harry & Hubendick, 1964); 4, Guadeloupe (Paraense, Fauran & Courmes, 1964); 5, Brésil (São Paulo) (Paraense, Fauran & Courmes, 1964); 6, Uruguay (Figueiras, 1965); 7, Bahamas (Clench, 1963); 8, Uruguay (Figueiras, 1965); 9, Texas (Harry & Hubendick, 1964); 10, Argentine (Buenos Aires) (Strobel, 1874); 11, Texas (Brownsville) (Pilsbry, 1934); 12, Brésil (Parana) (Lucena, 1956); 13, Mexique (Aguayo, 1947); 14, Argentine (Rio Parana) (D'Orbigny, 1835); 15, Bahamas (Harry & Hubendick, 1964); 16, Uruguay (Figueiras, 1965); 17, Cuba (Aguayo, 1947); 18, Brésil (Pernambuco) (Morretes, 1949); 19, Saint Martin (Coomans, 1967); 20, Bolivie (Pain, 1950); 21, Cuba (Aguayo, 1947); 22, Brésil (Bahia) (Recluz, 1850); 23, Floride, Bermudes (Aguayo, 1947); 24, Brésil (Parana) (Morretes, 1949); 25, Texas, Floride (Heard, 1963); 26, Mexique (Kuiper, comm. pers.); 27, Paraguay (Kuiper, comm. pers.); 28, Cuba (Aguayo, 1947); 29, Uruguay (Figueiras, 1964); 30, Bermudes (Clench, 1936); 31, Vénézuéla (Baker, 1930); 32, Texas (Aguayo, 1947); 33, Costa Rica (Preston, 1907); 34, Géorgie du sud, Texas du sud (Hubendick, 1967); 35, Vénézuéla du nord, Colombie du nord (Hubendick, 1967); 36, Texas (Crosse, 1892); 37, Bonaire (Vernhout, 1914); 38, Floride, Texas (Aguayo, 1947); 39, Vénézuéla (Baker, 1930); 40, Guadeloupe (Pointier, 1974); 41, Sainte Lucie (Sturrock, 1975); 42, Texas, Floride (Heard, 1965); 43, Guadeloupe, Marie Galante (Kuiper, comm. pers.); 44, Barbade (Kuiper, comm. pers.).

part, il se pose toujours le problème de la synonymie. Les nombreuses descriptions d'espèces étaient basées uniquement sur les caractéristiques conchyliologiques et, de ce fait, une certaine confusion règne dans la plupart des familles de



Légendes des cartes de répartition. (Les numéros correspondent à ceux de la liste des stations.)

Carte 1. Gites à *Biomphalaria glabrata*

Guadeloupe (Basse Terre): 2, 4, 5, 6, 7, 11, 12, 13, 14, 16, 19, 20, 22, 24, 25, 27, 29, 33, 34, 35, 37, 40, 49, 50, 55, 56, 57, 59, 61, 63, 64, 65, 67, 68, 70, 72, 73, 74, 78, 86, 87, 89, 92, 93, 94, 95, 99, 101, 108, 113, 116, 119, 124, 126, 140, 152, 157, 162, 163.

Grande Terre: 1, 2, 3, 4, 5, 7, 9, 10, 11, 13, 16, 17, 18, 19, 20, 21, 22, 23, 24, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 41, 42, 44, 45, 46, 49, 50, 51, 54, 55, 56, 57, 58, 59, 61, 63, 64, 65, 67, 68, 69, 71, 74, 75, 76, 77, 79, 81, 85, 86, 87, 88, 92, 93, 94, 96.

Marie Galante: 3, 4, 5, 6, 7, 9, 10.

Désirade: 1.

Carte 2. Gites à *Physa marmorata*

Guadeloupe (Basse Terre): 1, 2, 3, 4, 7, 8, 13, 15, 17, 19, 29, 31, 32, 33, 34, 36, 37, 40, 42, 50, 53, 54, 56, 57, 58, 61, 62, 63, 64, 68, 69, 72, 73, 78, 79, 81, 86, 87, 89, 90, 92, 93, 95, 96, 97, 98, 99, 100, 101, 102, 103, 104, 105, 106, 110, 111, 113, 114, 121, 124, 126, 128, 129, 130, 134, 135, 140, 152, 156, 161, 162, 163.

Grande Terre: 4, 5, 8, 10, 11, 12, 15, 16, 17, 18, 20, 21, 22, 26, 28, 32, 34, 35, 36, 38, 41, 42, 44, 51, 52, 55, 56, 58, 59, 60, 61, 65, 66, 68, 69, 70, 71, 74, 76, 77, 79, 82, 85, 86, 87, 88, 89, 92, 94, 95, 96, 97.

Désirade: 1.

Saintes: 1, 2.

Carte 3. Gites à *Ampullaria glauca*

Guadeloupe (Basse Terre): 5, 6, 9, 10, 18, 21, 22, 23, 24, 26, 28, 30, 32, 36, 38, 39, 41, 43, 44, 45, 46, 47, 48, 50, 51, 52, 53, 55, 56, 63, 65, 66, 67, 69, 71, 75, 76, 78, 80, 82, 84, 85, 87, 88, 89, 91, 98, 108, 112, 113, 122, 123, 124, 125, 127, 130, 132, 134, 135, 138, 141, 142, 144, 146, 147, 149, 150, 151, 154, 155, 156, 158, 159, 160, 161, 164.

Grande Terre: 3, 6, 8, 11, 16, 18, 19, 21, 23, 25, 28, 31, 34, 37, 40, 41, 42, 43, 46, 47, 56, 63, 68, 69, 74, 75, 92, 94.

Marie Galante: 4, 8, 10.

Carte 4. Gites à *Drepanotrema lucidum* (●)

Guadeloupe (Basse Terre): 83, 118.

Grande Terre: 11, 12, 16, 20, 22, 23, 24, 27, 28, 30, 32, 34, 35, 36, 38, 41, 44, 45, 48, 51, 52, 56, 59, 61, 62, 64, 65, 66, 68, 70, 71, 72, 73, 74, 76, 77, 78, 83, 84, 87, 88, 92, 96.

Marie Galante: 5, 6, 7.

Gites à *Neritina virginea* (▲)

Guadeloupe (Basse Terre): 63, 137, 139, 143, 144, 149, 151.

Grande Terre: 6, 86, 97.

Marie Galante: 1.

Gites à *Neritina succinea* (■)

Guadeloupe (Basse Terre): 139, 144, 149, 158.



Légendes des cartes de répartition. (Les numéros correspondent à ceux de la liste des stations.)

- Carte 5. Gites à *Drepanotrema hermatoides* (●)
 Guadeloupe (Basse Terre): 90, 92, 109. Grande Terre: 9, 11, 12, 16, 18, 22, 24, 28, 29, 30, 31, 34, 35, 38, 41, 42, 44, 45, 52, 56, 58, 60, 61, 64, 66, 68, 69, 70, 74, 77, 78, 84, 86, 88, 89, 94, 95. Marie Galante: 6, 7.
 Gites à *Neritina punctulata* (▲)
 Guadeloupe (Basse Terre): 60, 77, 126, 133, 137, 139, 142, 144, 145, 148, 149, 151.
 Gites à *Drepanotrema anatinum* (■)
 Guadeloupe (Basse Terre): 113, 120. Grande Terre: 82.
- Carte 6. Gites à *Potamopyrgus coronatus* (▲)
 Guadeloupe (Basse Terre): 2, 20, 36, 48, 57, 59, 61, 62, 63, 69, 124, 126, 131, 136, 140, 142, 143, 153, 155, 156, 159, 162, 163, 164. Grande Terre: 22, 23, 50, 69, 86, 88, 93, 97. Marie Galante: 1, 10.
 Gites à *Biomphalaria schrammi* (●)
 Guadeloupe (Basse Terre): 53, 92, 117, 118. Grande Terre: 11, 23, 31, 35, 42, 60, 68, 80, 84, 92, 96.
 Gites à *Drepanotrema aeruginosum* (■)
 Grande Terre: 56, 90, 91, 92.
- Carte 7. Gites à *Eupera viridans* (●)
 Guadeloupe (Basse Terre): 92. Grande Terre: 11, 16, 29, 32, 34, 35, 29, 41, 42, 45, 50, 51, 56, 61, 66, 96.
 Gites à *Pisidium punctiferum* (▲)
 Guadeloupe (Basse Terre): 53, 56, 61, 63, 83, 120. Grande Terre: 90.
 Gites à *Helisoma foveale* (○)
 Guadeloupe (Basse Terre)*
 Gites à *Dreissena* sp. (■)
 Grande Terre: 34. Marie Galante: 2.
- Carte 8. Gites à *Gundlachia radiata* (●)
 Guadeloupe (Basse Terre): 32, 48, 53, 55, 63, 73, 84, 102, 107, 115, 122, 146, 162. Grande Terre: 12, 16, 29, 34, 41, 48, 56, 92.
 Gites à *Lymnaea cubensis* (■)
 Grande Terre: 18, 23, 53, 88, 90.
 Gites à *Pleisiophysa granulata* (▲)
 Grande Terre: 11, 28, 32, 34, 35, 41, 42.
 Gites à *Physa cubensis* (□)
 Guadeloupe (Basse Terre): 25, 63, 126. Grande Terre: 2, 4.
 Gites à *Drepanotrema cimex* (○)
 Grande Terre: 16.

* Cette espèce avait été signalée en 1969 dans la rivière aux Herbes à Basse Terre. Elle n'a pas été retrouvée depuis.

LISTE DES STATIONS PROSPECTEES DE L'ARCHIPEL GUADELOUPEEN

(Les coordonnées A et B donnent la localisation des biotopes sur les cartes de répartition)

Guadeloupe (Basse Terre)

1, Affluent de la rivière La Rate A28-B9; 2, Ancienne piscine de Dolé A12-B14; 3, Bassin du château d'eau de Trois Rivières A12-B16; 4, Bassin à Cousinière A14-B10; 5, Bassin de la Distillerie Biglette A23-B16; 6, Bassin de la Distillerie Bonne Mère A25-B13; 7, Bassin de la Distillerie Fromager A15-B16; 8, Bassin de la Distillerie Jaula A25-B14; 9, Bassin de la Distillerie Montebello A20-B17; 10, Bassin de la Distillerie Routa A24-B15; 11, Bassin à Grand Camp A12-B13; 12, Bassin à Grand Croix A14-B9; 13, Bassin de l'Ilet A12-B12; 14, Bassin de réception de la Rivière Salée A26-B11; 15, Bassin à Saint-Claude A12-B13; 16, Bras mort de la Grande Rivière à Goyaves à la Boucan A26-B13; 17, Bras mort de la Rivière Bonfils A18-B17; 18, Bras mort de la Rivière à Goyaves à Bois Sec A18-B17; 19, Canal de l'Anse à la Fontaine A13-B18; 20, Canal de Bananier A13-B17; 21, Canal du Bas Carrère A21-B17; 22, Canal de Basse Terre-Pères A12-B11; 23, Canal de Bergnolles A23-B14; 24, Canal de Boisbert A25-B14; 25, Canal du Bois de Boulogne A14-B11; 26, Canal du Bois Sergent A20-B16; 27, Canal de Bonfils A25-B15; 28, Canal de Boyer A28-B12; 29, Canal de Campy A13-B11; 30, Canal de Cantamerle A13-B18; 31, Canal de Capesterre A15-B19; 32, Canal de Carrère A20-B17; 33, Canal de Circonvallation A11-B12; 34, Canal de Claire Fontaine A14-B11; 35, Canal de Dain A12-B12; 36, Canal de Daubin A24-B16; 37, Canal de la Distillerie Bellevue A13-B11; 38, Canal de la Distillerie Bonfils A24-B16; 39, Canal de la Distillerie Bourdon A24-B15; 40, Canal de la Distillerie Bovis A14-B10; 41, Canal de la Distillerie du Comte de Lohéac A29-B11; 42, Canal de la Distillerie Damoiseau A23-B16; 43, Canal de la Distillerie Diavet A27-B12; 44, Canal de la Distillerie Espérance A16-B18; 45, Canal de la Distillerie Fortyl A19-B17; 46, Canal de la Distillerie La Lise A20-B8; 47, Canal de la Distillerie Marsolle A25-B12; 48, Canal de la Distillerie Mon Repos A16-B18; 49, Canal de la Distillerie Montebello A21-B16; 50, Canal de la Distillerie Montplaisir A26-B15; 51, Canal de Dupuy A24-B16; 52, Canal de Duquerry A21-B16; 53, Canal des Galbas A27-B14; 54, Canal de Grande Anse A10-B14; 55, Canal de Grosse Montagne A24-B13; 56, Canal de l'Habitation Blachon A26-B16; 57, Canal de l'Habitation Bois Debout A14-B17; 58, Canal de l'Habitation Dumanoir A14-B15; 59, Canal de l'Habitation Georgie A14-B17; 60, Canal de l'Habitation Grivelière A15-B11; 61, Canal de l'Habitation A13-B18; 62, Canal de l'Hotel Thermal de Dolé A11-B14; 63, Canal de Marigot A17-B9; 64, Canal des Mineurs A14-B18; 65, Canal de Mon Repos A24-B16; 66, Canal de Montebello A21-B16; 67, Canal de Montinol A24-B17; 68, Canal du Moulin de la Coulisse de Trois Rivières A11-B16; 69, Canal de Pères La Violette A11-B15; 70, Canal de Petite Sucrerie A16-B9; 71, Canal de Pierrette A23-B15; 72, Canal de Pigeon A19-B9; 73, Canal de Pintade A11-B11; 74, Canal de Poirier A20-B9; 75, Canal de Pont Mahaut A24-B17; 76, Canal de la Retraite A24-B16; 77, Canal de Roland A15-B9; 78, Canal de Roujol A22-B16; 79, Canal de Saint Louis A13-B12; 80, Canal de Saussaye A21-B16; 81, Canal de la Tombe Grand Croix A14-B10; 82, Canal de Trois Rivières A11-B15; 83, Canal du Val Kanaërs A11-B14; 84, Canal du Val de l'Orge A14-B10; 85, Canal de Victor Hugues A20-B16; 86, Canal de Vieux Habitants A15-B9; 87, Canal de Volny A24-B14; 88, Canal de Vounche A24-B16; 89, Embouchure de la Grande Rivière à Vieux Habitants A15-B9; 90, Etang Gommier A11-B15; 91, Fossé à l'Anse des Pères A10-B14; 92, Grand Etang A14-B15; 93, Infiltrations du canal de Bouvier A13-B12; 94, Infiltrations du canal de la Brigade A13-B11; 95, Infiltrations du canal de la Coulisse de Baillif A13-B11; 96, Infiltrations du canal de la Distillerie Bologne A12-B11; 97, Infiltrations du canal de la Distillerie Espérance A16-B14; 98, Infiltrations du canal de la Distillerie Tabanon A22-B14; 99, Infiltrations du canal de la Distillerie Valeau A14-B11; 100, Infiltrations du canal de Grand Croix A14-B10; 101, Infiltrations du canal de Grosse Montagne A23-B14; 102, Infiltrations du canal de La Lise A20-B9; 103, Infiltrations du canal du Pont Belcourt A25-B17; 104, Infiltrations du canal de Saussaye A21-B16; 105, Infiltrations du canal de la Sucrerie Roujol A21-B17; 106, Infiltrations du canal de Vanibel-Plessis A14-B11; 107, Infiltrations dans la Distillerie Montebello A21-B17; 108, Infiltrations de la Grande Rivière à Goyaves à Barbotteau A22-B13; 109, Infiltrations de la Grande Rivière à Vieux Habitants A15-B9; 110, Infiltrations à l'Habitation Grivelière A15-B11; 111, Infiltrations d'une Ravine à Schoelcher A11-B15; 112, Infiltrations de la Rivière Bonfils A18-B16; 113, Infiltrations de la Rivière Houaromond A25-B17; 114, Infiltrations du Ruisseau Montval A15-B11; 115, Mare à Barbotteau A22-B14; 116, Mare à Carrère A20-B16; 117, Mare de Mazeau no. 1 A26-B8; 118, Mare de Mazeau no. 2 A26-B8; 119, Mare à Vounche A25-B16; 120, Marécage à Barbotteau A22-B14; 121, Marécage à Basse-Terre-Pères A12-B10; 122, Ravine à la Boucan A26-B14; 123, Ravine à Caféière A28-B9; 124, Ravine Couleuvre A28-B8; 125, Ravine Favard A22-B16; 126, Ravine Grand Camp A17-B11; 127, Ravine La Fayette A23-B14; 128, Ravine Mazeau A27-B8; 129, Ravine Rocroy A14-B10; 130, Ravine à Sainte Rose A29-B12; 131, Rivière Acajou A23-B9; 132, Rivière de Bananier A13-B17; 133, Rivière Beaugendre A16-B10; 134, Rivière Bébel A28-B12; 135, Rivière Briquetterie A17-B18; 136, Rivière Caillou A24-B8; 137, Rivière Colas A21-B8; 138, Rivière Corossol A22-B13; 139, Rivière de Deshaies A27-B8; 140, Rivière Forban A28-B8; 141, Rivière Gombo A24-B12; 142, Rivière Mahaut A21-B8; 143, Rivière Petit Canal A14-B10; 144, Rivière Petite Plaine A23-B9; 145, Rivière des Pères A13-B10; 146, Rivière La Perle A29-B8; 147, Rivière La Rate A28-B8; 148, Rivière La Rose A18-B18; 149, Rivière Salée de Sainte Rose A28-B12; 150, Rivière Sans Nom A24-B16; 151, Rivière Ziotte A28-B8; 152, Ruisseau des Bains Jaunes A14-B13; 153, Ruisseau de Bas Vent A29-B9; 154, Ruisseau avant Belle Plaine A26-B13; 155, Ruisseau à Changy A16-B18; 156, Ruisseau à Deshaies A28-B8; 157, Ruisseau Grand Canal A14-B10; 158, Ruisseau à Montplaisir A27-B13;

159, Ruisseau à Morphy A25-B7; 160, Ruisseau de Petite Folie A22-B14; 161, Ruisseau à Pigeon A20-B9; 162, Ruisseau à Pinaud A29-B8; 163, Ruisseau La Plaine A12-B16; 164, Ruisseau de Pont Clémence à Fort-Royal A29-B8.

Grande Terre

1, Bassin de la Distillerie Berville A29-B24; 2, Canal du Boulevard Faidherbe à Pointe à Pitre A24-B20; 3, Canal Decostière A29-B22; 4, Canal du Faubourg Nozière à Pointe à Pitre A24-B20; 5, Canal Moreau A30-B24; 6, Canal Perrin A28-B21; 7, Canal de Pointe à Retz A31-B23; 8, Canal de Pont à Popo A27-B21; 9, Canal des Rotours A30-B23; 10, Canal de Vieux Bourg A29-B21; 11, Etang Cocoyer A28-B27; 12, Etang Secrétan A26-B29; 13, Fossé à Morne à l'Eau A30-B24; 14, Fossé à Pont à Popo A27-B21; 15, Infiltrations du Canal de Pointe à Retz A30-B24; 16, Mangrove de Devarieux A29-B23; 17, Mare de Acomat A29-B26; 18, Mare de Alphonse no. 1 A28-B28; 19, Mare de Alphonse no. 2 A28-B28; 20, Mare de l'Anse Bertrand A37-B21; 21, Mare de Banzon A25-B22; 22, Mare de Barbès A24-B22; 23, Mare de Bauvel A28-B27; 24, Mare de Bebian Baigner A35-B22; 25, Mare de Belcourt A26-B28; 26, Mare de Bellevue Babaie A36-B22; 27, Mare de Bois Normand A37-B24; 28, Mare de Borricaud A27-B24; 29, Mare de Caraque no. 1 A25-B21; 30, Mare de Caraque no. 2 A25-B21; 31, Mare de Caraque no. 3 A25-B21; 32, Mare de Céligny no. 1 A25-B23; 33, Mare de Céligny no. 2 A25-B23; 34, Mare de Céligny no. 3 A25-B23; 35, Mare de Champvert A24-B23; 36, Mare de Claret A28-B30; 37, Mare de Clugny A29-B26; 38, Mare de Cocoyer A24-B21; 39, Mare de Dampierre A23-B23; 40, Mare de Deshauteurs no. 1 A25-B24; 41, Mare de Deshauteurs no. 2 A25-B24; 42, Mare de Deshauteurs no. 3 A25-B24; 43, Mare de la Distillerie Delisle A31-B24; 44, Mare de la Distillerie Devarieux A29-B23; 45, Mare de Dubisquet no. 1 A28-B24; 46, Mare de Dubisquet no. 2 A28-B24; 47, Mare de Dubois A25-B23; 48, Mare de Durivage A24-B27; 49, Mare de Eucher A24-B25; 50, Mare de Fauvette no. 1 A33-B20; 51, Mare de Fauvette no. 2 A33-B20; 52, Mare de Fouché A25-B27; 53, Mare de French Distillerie A25-B26; 54, Mare de Geffrier A29-B22; 55, Mare de Gentilly A26-B28; 56, Mare de Goudenaves A24-B23; 57, Mare de Grande Ravine A23-B24; 58, Mare de Gros Cap A33-B27; 59, Mare de Guillon A24-B25; 60, Mare de Jalousie no. 1 A26-B24; 61, Mare de Jalousie no. 2 A26-B24; 62, Mare de Lamarre A25-B26; 63, Mare de Lambert A25-B22; 64, Mare de Le Roux A24-B22; 65, Mare du Lotissement du Vieux Moulin A29-B30; 66, Mare de Louisiane A26-B26; 67, Mare de Mahaudière A35-B24; 68, Mare de Malabry A27-B24; 69, Mare des Mangles A33-B24; 70, Mare de Marie Thérèse A35-B24; 71, Mare de Mathurin A24-B21; 72, Mare du Moulin Belcourt A25-B29; 73, Mare du Moulin Loery A26-B29; 74, Mare de Philémon A25-B22; 75, Mare de Pico A30-B23; 76, Mare de la Porte d'Enfer du Moule A29-B31; 77, Mare de Radier A30-B24; 78, Mare de Redbone A23-B24; 79, Mare de Réjoui A24-B21; 80, Mare de Saint-Jacques A37-B23; 81, Mare de Sainte Marguerite A31-B25; 82, Mares de Sainte Rose A27-B29; 83, Mare de Senneville A35-B21; 84, Mare de Séo A25-B30; 85, Marécage de Damencourt A29-B28; 86, Marécage à Gosier A23-B22; 87, Marécage du Moulin Monmain A24-B29; 88, Marécage de Port Louis A34-B20; 89, Marécage de Ramier A29-B25; 90, Prairie inondée à Devarieux A29-B23; 91, Prairie inondée à Sainte Marguerite A31-B25; 92, Ravine des Coudes A30-B26; 93, Ravine Gachette A33-B21; 94, Ravine Nègresse A28-B26; 95, Ravine à Petit Pérou A25-B21; 96, Ruisseau à Favreau A26-B31; 97, Ruisseau à Gosier A23-B21.

Marie Galante

1, Embouchure de la Rivière de l'Anse Vieux Fort A12-B32; 2, Marais de Fosse Anse A9-B30; 3, Mare Bamhou A10-B33; 4, Mare à Dorot A12-B33; 5, Mare de Ducas A8-B32; 6, Mare à Grand Bourg A7-B31; 7, Mare au Punch A8-B33; 8, Mare de Sainte Croix A9-B33; 9, Mare de Trianon A8-B31; 10, Marécage de Vangout A12-B32.

Saintes

1, Mare de l'Anse Rodrigue A4-B18; 2, Mare du Terrain d'Aviation A5-B18.

Désirade

1, Source à Baie Mahaut A30-B45.

Mollusques d'eau douce. C'est pourquoi pour quelques espèces il est difficile, voire même parfois impossible, de préciser leurs limites de répartition; ainsi, dans le Tableau 3, qui essaie de préciser pour chaque Mollusque guadeloupéen ses limites d'extension géographique dans les hémisphères nord et sud, nous pouvons observer par exemple que pour *Biomphalaria schrammi*, seules les données de Paraense, Fauran & Courmes (1964) pour la Guadeloupe au nord, et le Brésil au sud, paraissent sûres. *B. schrammi* serait très proche d'une autre espèce, *B. helophila*. La ressemblance des coquilles des 2 espèces est telle qu'il est impossible de les distinguer, et seul l'appareil génital permet la différenciation (Paraense, Fauran & Courmes, 1964). Chez *B. schrammi*, en effet, le fourreau du penis

est "au minimum quatre fois plus long que le prépuce" alors que chez *B. helophila*, celui-ci est "aussi long, jusqu'à quatre fois plus long que le prépuce." Ces critères de différenciation établis par Paraense peuvent paraître sujets à caution car on voit mal en cas de variabilité morphologique importante, la différence qu'il pourrait y avoir entre un *B. helophila* dont le sac du penis est "au plus quatre fois plus long" que le prépuce et un *B. schrammi* dont le sac du penis est "au minimum quatre fois plus long." Seule une étude approfondie sur des populations de Mollusques d'origines diverses pourrait apporter des éclaircissements. Quoiqu'il en soit, *B. schrammi* et *B. helophila* ont certainement été confondus dans de nombreuses régions par les malacologistes sous les dénominations diverses de *Planorbis albicans*, *P. janeirensis*, *P. dentiferus*, etc. Les limites de répartition de l'espèce *helophila* sont au nord, la Louisiane et le Texas (Harry & Hubendick, 1964), et au sud, l'Uruguay (Figueiras, 1965).

Les autres Planorbidae du genre *Drepanotrema* et *Helisoma* ont également une répartition assez large puisque on les trouve en général, du sud des U.S.A. jusqu'en Uruguay et en Argentine. Seul, *H. foveale* ne paraît pas dépasser au sud, l'Amérique Centrale malgré les références de Cousin (1887) sur l'Equateur et de Broderip (1832) sur le Pérou qui n'ont pas été confirmées depuis.

En ce qui concerne les autres espèces, il convient de noter les distributions complémentaires des 2 espèces de *Physa*: *Physa cubensis* est déjà présente aux Bermudes et au sud des U.S.A. (Clench, 1936), mais ne semble pas dépasser le 12^e parallèle où la dernière référence est donnée par Baker (1930) au Vénézuéla; par contre, si l'aire de *P. marmorata* débute seulement à Cuba (Aguayo & Jaume, 1947), elle se termine dans l'hémisphère sud en Uruguay (Figueiras, 1964). L'aire commune de répartition des 2 espèces serait donc restreinte à la zone Caraïbe. Cependant, il faut remarquer que la distinction des 2 *Physa* est délicate lorsqu'on se fie uniquement aux caractéristiques conchyliologiques, et seuls les critères anatomiques peuvent permettre la détermination des 2 espèces avec certitude (Harry & Hubendick, 1964). Il est donc possible que des confusions se soient produites et là encore, il convient d'être prudent vis à vis de certaines références empruntées à la littérature.

L'espèce guadeloupéenne la moins répandue dans la zone néotropicale est *Neritina succinea*. Elle n'a été récoltée seulement qu'à Sainte Lucie (Sturrock, 1975), mais il est probable que cette petite nérítine est présente dans d'autres îles ou même sur le continent, car elle ne paraît pas avoir de biotope particulier à Sainte Lucie ou à la Guadeloupe. On la trouve, en effet, dans les rivières et les ruisseaux courants en compagnie ou non des autres nérítines.

Pisidium punctiferum et *Eupera viridans* sont 2 petits lamellibranches très communs en Guadeloupe. Là encore, il est difficile d'établir avec précision les limites de leur répartition géographique à cause du manque de données confirmées et du problème de la synonymie. *Pisidium punctiferum* paraît avoir une aire de répartition beaucoup plus vaste que *E. viridans*. Kuiper (comm. pers.) a effectué les déterminations de séries de *P. punctiferum* provenant de Trinidad, Cuba, Mexique et Jamaïque, et, en 1973, a eu l'occasion de réviser quelques collections du Museum of Comparative Zoology, Harvard University (*P. punctiferum* provenant du Vénézuéla, du Mexique, de la Jamaïque et du Paraguay), ainsi que du American Museum of Natural History de New York (*P. punctiferum* de Cuba). Par ailleurs, Heard (1963) signale *P. punctiferum* au Texas, en Floride (?), au Mexique, au Guatemala, à Panama, Cuba et Trinidad. Par contre, les références de Herrington (1962) et de Heard (1962) relatives à la présence de l'espèce en Amérique du Nord (Grand Lacs), et en Europe sont fausses par suite d'erreurs synonymiques (Kuiper, 1962).

En ce qui concerne *Eupera viridans*, les données sont plus rares. Selon Kuiper

(comm. pers.), cette espèce serait probablement synonymique à l'*Eupera parvulum* (Prime 1865) de Porto Rico, l'*E. barbadensis* (Prime 1861) de la Barbade, et peut être de l'*E. cubensis* (Prime 1865) de Cuba, lequel aurait selon Heard (1965), une répartition assez large au sud des U.S.A. (Floride, Alabama, Mississippi, Texas).

CONCLUSION

Aucun Mollusque d'eau douce, parmi ceux qui ont été récoltés en Guadeloupe, n'est endémique. Malgré le manque de références pour certaines régions, la faune guadeloupéenne paraît assez bien représentée dans les Caraïbes ainsi qu'en Amérique Centrale et du Sud. C'est ainsi que du sud des U.S.A. au sud du Brésil, les pays ou les îles ayant fait l'objet de recherches approfondies ont une faune malacologique comprenant la plupart des espèces guadeloupéennes: Texas, Floride, Mexique, Vénézuéla, Brésil, Cuba, Hispaniola, Porto Rico, Martinique, Sainte Lucie (sur les 21 espèces présentes en Guadeloupe (16°N), 13 ont une aire de répartition qui s'étend jusque dans l'hémisphère sud).

Si l'on considère les Petites Antilles, la Guadeloupe présente la faune la plus complète de l'archipel. Ce phénomène est compréhensible si l'on sait que la Guadeloupe est un système insulaire formé de 2 îles très différentes du point de vue géologique et climatique. Ainsi, la diversité des biotopes offerts par les 2 îles ne se retrouve dans aucune autre des Petites Antilles. La faune malacologique guadeloupéenne serait plutôt comparable à celle des Grandes Antilles, Cuba, Hispaniola, et surtout Porto Rico. Par ailleurs, elle garde la caractéristique de l'insularité en étant incomparablement moins riche que celle du continent. C'est ainsi que pour la seule famille des Planorbidae, 3 ou 4 espèces de *Biomphalaria* ont été recensées dans les Antilles (2 en Guadeloupe), alors qu'une vingtaine est signalée en Amérique du Sud (cf. Pan. Amer. Hlth. Org., 1968).

ABSTRACT

The distribution of the 21 species of freshwater molluscs of Guadeloupe was studied. Three groups of species were distinguished: running water species, stagnant water species and ubiquitous species. The most common species are *Biomphalaria glabrata*, intermediate host of *Schistosoma mansoni*, *Ampullaria glauca* and *Physa marmorata*. A comparison of the habitats of these 3 species shows that *B. glabrata* and *P. marmorata* tolerate each other in several biotopes. In contrast, the partial exclusion which seems to exist between *B. glabrata* and *A. glauca* is perhaps caused by the latter species' preference for fast moving water.

No freshwater mollusc is endemic to Guadeloupe, and most species are widely distributed in the northern hemisphere and also in the southern hemisphere, where 13 of the 21 Guadeloupe species can be found.

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THREE SPECIES OF LITTORINIDAE FROM SOUTHERN AUSTRALIA

W. F. Ponder

ABSTRACT

Two species (*Macquariella kingensis* and *Rufolacuna bruniensis*) previously placed in the Naticidae and Cyclostrematidae, respectively, are transferred to the Littorinidae. *Laevilitorina burni* sp. nov. and *Rufolacuna* gen. nov. are newly described. The suggestion is made that the Lacunidae be included within the Littorinidae as a subfamily.

Current investigations on algal-living micro-Mollusca have revealed 3 species which can be included in the Littorinidae, 1 of which was previously described as a naticid, another as a cyclostrematid and the 3rd is new.

TAXONOMY

Family Littorinidae

Rosewater (1970) has included in his list of genera of the Littorininae a number of genera around *Laevilitorina* Pfeffer which he did not deal with in further detail. Powell (1951) provided the major contribution to the classification of the *Laevilitorina* group which, he showed, has a remarkable diversity in the details of radular pattern. Several species in this group are umbilicate and, presumably for this reason, some have been associated with the Lacunidae by early workers.

An assessment of the familial characters of the Lacunidae and the Littorinidae shows that they do not have any significant differences in anatomy, radular features or spawn (Fretter & Graham, 1962); the only differences normally cited are the umbilicate, lightly built shell, their low-tidal habit and the presence of metapodial tentacles. The presence or absence of metapodial tentacles is a highly variable feature in the littorinacean family Eatoniellidae, where it is not even indicative of generic groups (Ponder, 1965). For this reason, and because these structures have not been demonstrated in the majority of lacunids, little reliance can be placed on them as a family-level character. The presence or absence of an umbilicus is hardly a character of family-level importance. Species in the *Laevilitorina* group, for example, show considerable variation from a widely umbilicate to an imperforate condition.

It is probable that the *Lacuna* group are primitive littorinids, particularly in view of their metapodial tentacles, unspecialized habits and shell. The most satisfactory solution at present would be to regard the *Lacuna* group as a subfamily of the Littorinidae. The *Laevilitorina* group could be tentatively retained in the Littorininae, although the only obvious feature that could be used to separate them from the Lacuninae is the absence of metapodial tentacles.

Genus *Laevilitorina* Pfeffer 1886

Type species (subsequent designation Suter 1913), *Littorina calignosa* Gould 1849.

Diagnosis: Shell small, ovate-conical, imperforate or very narrowly umbilicate, periostracum smooth. Radula with narrow central tooth, central and lateral teeth with several prominent, narrowly pointed cusps, marginals fan-shaped and multi-denticulate (slightly modified from Powell, 1951: 106). Head-foot simple. Penis (of type species) elongate, oval in section, evenly tapering, with no accessory glandular structures. A longitudinal groove from base along about 1/4 of total length (text Fig. 11).

Remarks: The new species described below fits the generic diagnosis given by Powell (1951) moderately well. There are a few, mainly rather subtle, shell characters of the type species that do not agree well with the new species and the opercula are differently coiled, but in view of the perhaps immature condition of the material being described here as new, this somewhat tentative generic allocation is allowed.

The only other Australian species included in *Laevilitorina* is *Rissoa mariae* Tenison-Woods 1876, and this has been transferred to *Rissolittorina* Ponder 1966 (type species *Zelaxitas alta* Powell 1940) by Ponder (1966).

Laevilitorina burni sp. nov.

Text Fig. 8; Pl. 1, Fig. 1; Pl. 2, Figs. 5, 6

Shell: Minute, conical, yellowish-white, imperforate, with large aperture and blunt protoconch. Protoconch of $1\frac{1}{4}$ - $1\frac{1}{2}$ whorls, bluntly rounded, last $\frac{1}{2}$ whorl swollen and projecting slightly beyond line of spire; teleoconch of up to 2 slightly convex whorls. Sutures weakly impressed, false margined. Aperture large, posterior corner slightly advanced, anterior corner projecting, anterior edge nearly flat, slightly excavated. Outer lip thin, simple, inner lip a thin glaze over columella and parietal area. Columella prominent, straight, oblique. Umbilicus absent. Surface smooth, shining, with very weak, close growth lines and indistinct close spiral scratches. Pale yellowish-white, lower base and columella white. Periostracum thin, transparent (text Fig. 8).

Dimensions: Length 2.0 mm, diameter 1.68 mm (holotype).

Operculum: Simple, nucleus markedly abcentric, pale yellow, transparent (Pl. 2, Figs. 5, 6).

Radula: Central teeth each with a rather long, sharp median cusp and a pair of small lateral cusps on the narrow cutting edge. Lateral teeth each with 2 small cusps on either side of the moderately large median cusp. Inner marginal teeth each with 2 moderate-sized inner cusps, a slightly larger median cusp and a small outer cusp. Outer marginals with about 10 small, sharp cusps of equal size (Pl. 1, Fig. 1). Radular sac long, coiled.

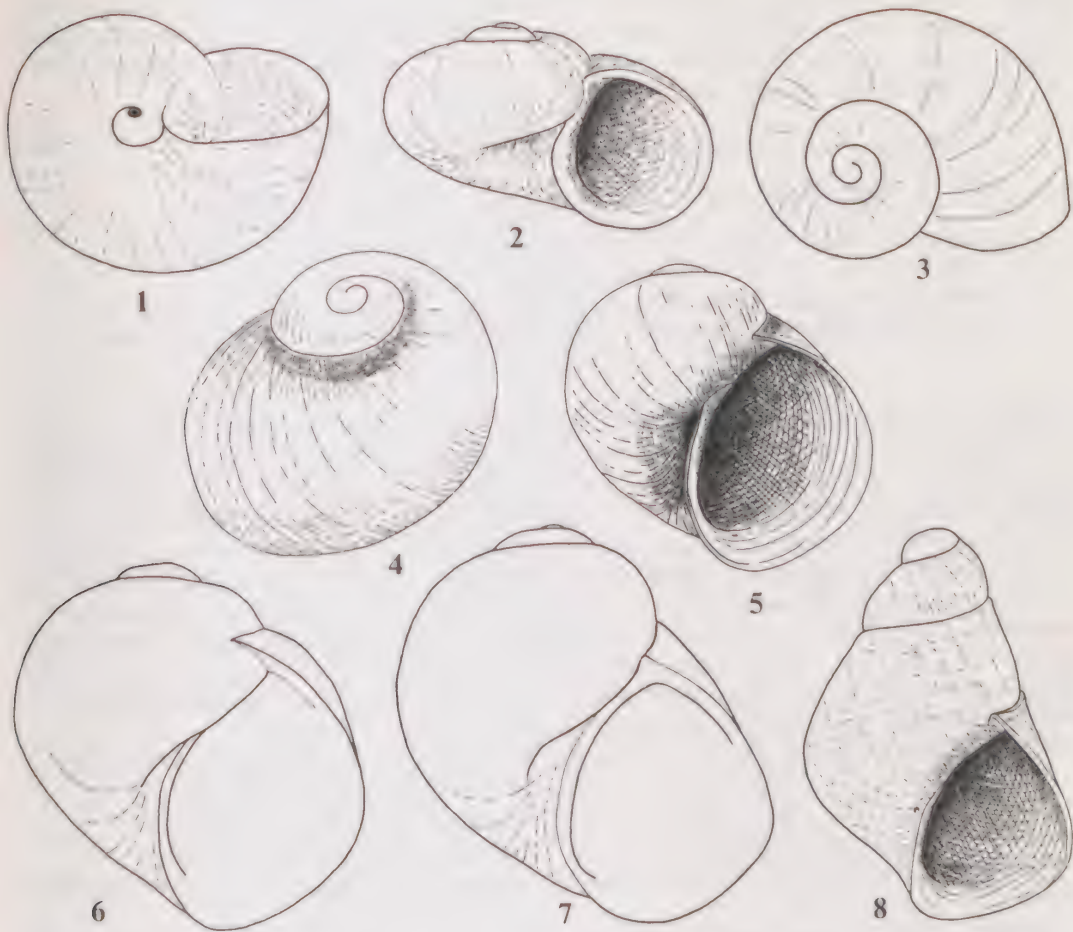
Head-foot: Unpigmented, snout and tentacles as in the other 2 species described herein. A posterior mucous slit in sole and a mucous slit on anterior edge of foot well developed. There do not appear to be any metapodial tentacles (preserved material from both localities).

Types: Holotype (C. 100919) and 9 paratypes (C. 100920, C. 100921), AM¹ and 3 paratypes WAM.

Type Localities: Yallingup, southwestern Australia, on limestone platform living on algae, 1 January 1972, coll. W. F. Ponder and B. R. Wilson. Holotype (C. 100919) and 8 paratypes (5 AM, C. 100920; 3 WAM). South Point, south of Two People's Bay, near Albany, southwestern Australia, on large brown algae on exposed shore, 3 February 1972, coll. W. F. Ponder. Four dry paratypes (C. 100921) and 3 remains of animals (not regarded as paratypes).

Remarks: A total of 6 specimens from the 2 localities were crushed and their preserved animals examined. Although some were of equal size to the type (others were smaller), all appeared to be sexually immature and aphyllate. It is, however, unlikely that this species reaches a much larger size than the holotype.

¹Abbreviations: AM, Australian Museum, Sydney; NMV, National Museum of Victoria, Melbourne; TM, Tasmanian Museum, Hobart; WAM, Western Australian Museum, Perth; SEM, scanning electron microscope; pres., presented by; coll., collected by.



FIGS. 1-8. Shells. FIGS. 1-3. *Rufolacuna bruniensis* (Beddome). Ventral, lateral and dorsal views of shell. Derwent River Estuary, Tasmania, pres. W. L. May (AM C. 10782). FIGS. 4-7. *Macquariella kingensis* (May). FIGS. 4, 5. Flinders, Victoria, ocean platform, coll. B. J. Smith (AM C. 100925). FIGS. 6, 7. Paratypes (AM C. 49554). FIG. 8. *Laevilitorina burni* sp. nov., holotype.

The new species differs from other species of *Laevilitorina* in its distinctly conical form, subangled periphery and in the complete absence of an umbilicus or umbilical chink. The pale yellow colour is also distinctive, most species being brown. It is named for Mr. R. Burn of Geelong as a small gesture of appreciation for his companionship in the field and help in many other ways.

Genus *Macquariella* Finlay 1927

Type species (original designation) *Paludestrina hamiltoni* Smith 1898.

Diagnosis: Shell naticiform, subglobose, narrowly umbilicate, smooth, simple. Radula with narrow-necked central teeth, each having 2 small cusps on either side of a larger, rather blunt median cusp. Lateral teeth each with broad, straight cutting edge with 4-5 small cusps on inside of 2 larger cusps; inner marginal teeth each with a straight row of about 9 teeth, the second to outermost tooth slightly

larger. Outer marginal teeth multidenticulate. Operculum simple, paucispiral, nucleus abcentric. Head-foot simple, snout rather long, broad, opercular lobes simple (type species pigmented dark grey head and foot). Penis simple, with a slit along its proximal half (text Figs. 13, 13a).

Macquariella kingiensis (May 1924)

Text Figs. 4-7, 9, 10; Pl. 1, Fig. 3; Pl. 2, Figs. 7, 8

Cyclostrema kingi (Brazier ms.) Tenison-Woods 1877: 39; Tate & May, 1901: 445; Hedley, 1913: 300. *Nomen nudum*.

Natica kingensis May 1924: 49, pl. 7, figs. 3, 3a.

Notocochlis kingensis; Kershaw, 1955: 314; Macpherson, 1958: pl. 48, figs. 3, 3a.

Shell: Small, thin, naticiform, with depressed spire, last whorl bulbous, aperture large, narrowly umbilicate. Protoconch weakly convex, of 1 1/2 whorls, teleoconch of up to 2 1/4 convex whorls, sutures adpressed. Last 1/2 whorl descends rather rapidly in large specimens. Aperture large, oval, inner lip a thin glaze over columella and parietal area in juveniles, thickened and semidetached in mature shells. Outer lip advanced posteriorly, edge thin, simple, slightly thickened internally and excavated anteriorly. Columella prominent, long, subvertical, slightly concave. Umbilicus small, relatively larger in mature shells than in immature specimens. Surface smooth except for very weak, close, axial growth lines. Pale horny yellow except for umbilical area, lower inner lip and a narrow line below suture which are reddish-brown (text Figs. 4-7).

Dimensions: Length 2.50 mm, diameter 2.00 mm (from original description)

2.50 mm	2.00 mm (figured paratype)
2.22 mm	1.88 mm (figured paratype)
1.87 mm	1.80 mm (figured specimen)

Operculum: Simple, of about 2 whorls, nucleus abcentric, pale yellow, transparent (Pl. 2, Figs. 7, 8).

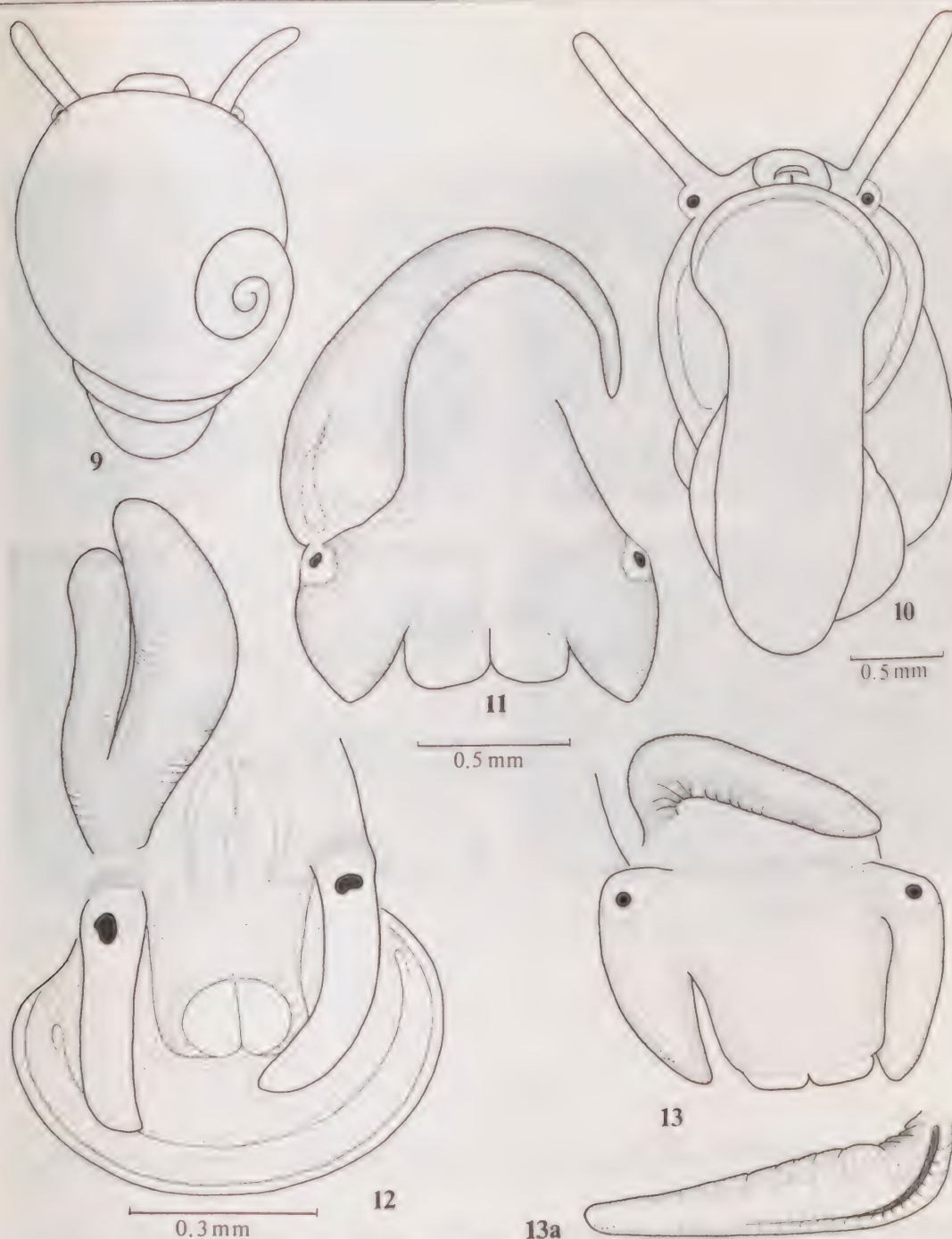
Radula: Central teeth each with 2 small cusps on either side of a rather blunt median cusp. Lateral teeth each with 4 cusps on inside of a pair of larger cusps on outer end of a long, straight cutting edge. Inner marginal teeth each with 8-10 cusps, primary cusp second from outside, all arranged in a rather straight row. Outer marginal teeth each with about 9 minute cusps of equal size (Pl. 1, Fig. 3).

Head-foot: Living animal with a rather short, broad foot, sole simple, lacking posterior mucous gland slit; transverse opening of the anterior mucous gland on anterior end of sole; opercular lobes simple, cephalic tentacles rather long, constantly mobile, with parallel sides and with the eyes in bulges at their outer bases. Snout moderately long. Colour of head-foot pale yellowish-brown dorsally, tentacles pale yellow, sole dirty white. Buccal mass pink, snout pale brown, distal end yellowish-white (specimens from Lorne) (text Figs. 9, 10). All specimens examined immature and aphyllate.

Types: Syntypes (4) TM (E585/7926), paratypes (9) AM (C. 49554).

Type Locality: Currie Harbour, King Island, Bass Strait, in shell sand.

Material Examined: Paratypes (AM, C. 49554); King Island, Bass Strait (AM); 9-18 m, Fraser Bay, King Island, Bass Strait, coll. F. Basset Hull, 1922 (AM); Western Port, Victoria (AM; NMV); Flinders, Victoria (AM); Flinders, Victoria, ocean platform, low tide rock pools, coll. B. J. Smith, 1967 (AM); Point Grey, Lorne, Victoria, on large brown algae, exposed coast, coll. W. F. Ponder and R. Burn, 1975 (AM); south end of Green Cape, southern New South Wales, 2-4 m, exposed coast, on algae, coll. W. F. Ponder, 1973 (AM).



FIGS. 9-13. Morphological features. FIGS. 9,10. *Macquariella kingensis* (May). Dorsal (Fig. 9) and ventral (Fig. 10) views of the living animal. Point Grey, Lorne, Victoria (AM C. 100924). FIG. 11. *Laevilitorina calignosa* (Gould). Dorsal view of head and penis of preserved specimen. North Garden Cove, Macquarie Island, on algae, coll. R. Simpson, 20 October 1968 (AM C. 91936). FIG. 12. *Rufolacuna bruniensis* (Beddome). Dorsal view of head, foot and penis of preserved specimen. Fortescue Bay, eastern side of Tasman Peninsula, southeastern Tasmania (TM). FIGS. 13,13a. *Macquariella hamiltoni* (Smith). FIG. 13. Dorsal view of head and penis. FIG. 13a. Ventral view of penis (slightly enlarged). North Garden Cove, Macquarie Island, on algae, coll. R. Simpson, 20 October 1968 (AM C. 91928).



PLATE 1

FIG. 1. *Laevilitorina burni* sp. nov. Radula, x1200. Yallingup, southwestern Australia. SEM Stub 233, AM.

FIG. 2. *Rufolacuna bruniensis* (Beddome). Radula, x1600. Fortescue Bay, southeastern Tasmania. SEM Stub 232, AM.

FIG. 3. *Macquariella kingensis* (May). Radula, x1600. Point Grey, Lorne, Victoria. SEM Stub 178, AM.

FIG. 4. *Macquariella hamiltoni* (Smith). Radula, x900. North Garden Cove, Macquarie Island. SEM Stub 215, AM.

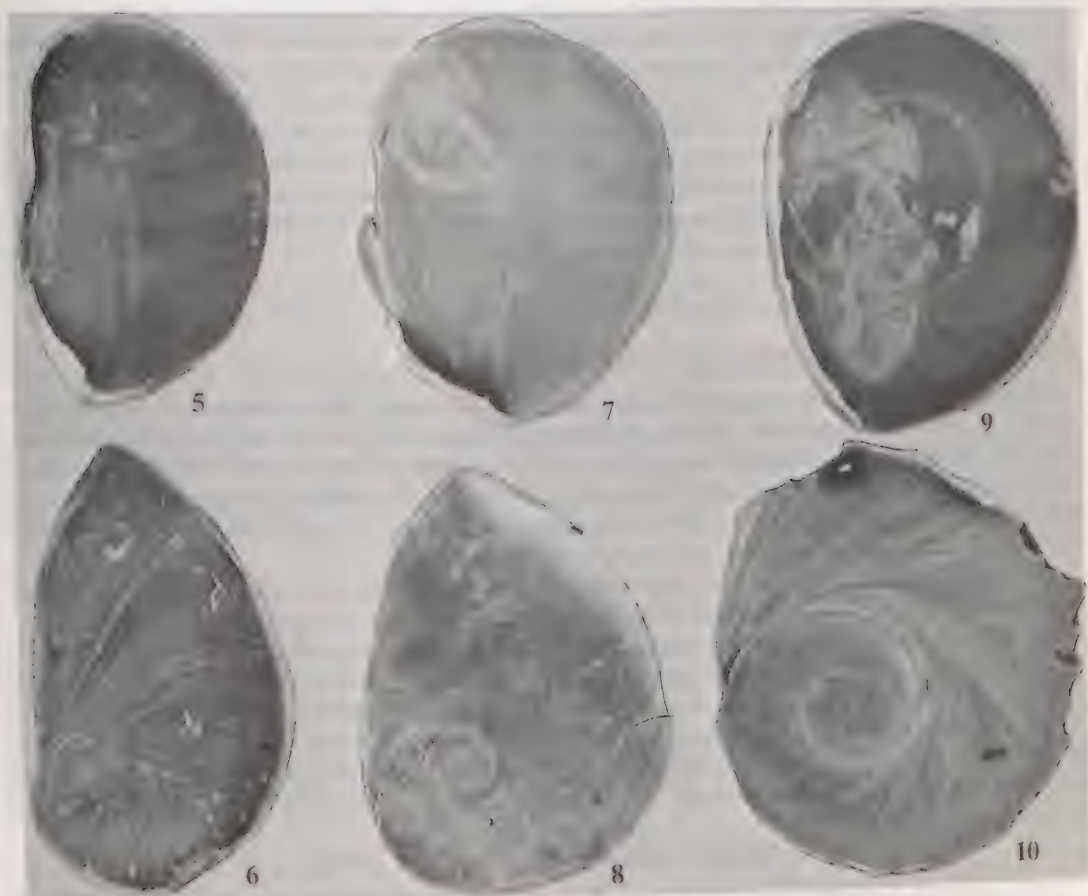


PLATE 2

FIGS. 5, 6. *Laevilitorina burni* sp. nov. Operculum. FIG. 5. Inside, x70. FIG. 6. Outside, x70. Yallingup, southwestern Australia. SEM Stub 233, AM.

FIGS. 7, 8. *Macquariella kingensis* (May). Operculum. FIG. 7. Inside, x55. FIG. 8. Outside, x55. Flinders on ocean platform. SEM Stub 62, AM.

FIG. 9. *Rufolacuna bruniensis* (Beddome). Operculum, x80 (inside). Fortescue Bay, southeastern Tasmania. SEM Stub 209, AM.

FIG. 10. *Macquariella hamiltoni* (Smith). Operculum, x35 (outside). North Garden Cove, Macquarie Island. SEM Stub 215, AM.

Remarks: This species has a remarkable resemblance to a small naticid in shape and closely resembles the common Australian naticid *Conuber conica* (Lamarck) in colour. It is thus not surprising that May described this species as a *Natica* and Hedley (1913) stated that it is the "youngest growth-stage" of the naticid *Glossaulax aulacoglossa* (Pilsbry & Vanatta).

The radula and shell of this species are similar to those of the type species of *Macquariella* but the radula differs considerably from that of *M. aucklandica* Powell as figured by Powell (1951).

This species differs from the other species of *Macquariella* chiefly in colour and minor details of shape. It is most similar to the type species from which it differs in colour, *M. hamiltoni* being uniform brown, and in the coiling of the operculum (cf. Pl. 2, Figs. 7, 8 and 10). It is the 1st species of this genus to be recorded outside southern New Zealand and the Subantarctic.

Rufolacuna gen. nov.

Type species *Cyclostrema brunensis* Beddome 1883.

Diagnosis: Shell depressed, much broader than high, with a wide umbilicus and deeply impressed sutures. Aperture simple with complete peristome. Operculum simple, paucispiral, nucleus abcentric. Radula similar to that of *Laevilitorina* except that the primary cusps lie towards the outer sides of the cutting edges of the lateral and inner marginal teeth. Penis with large, simple, elongate accessory glandular lobe attached near its proximal end.

Remarks: The shell of the type species of the new genus is distinguished from species of *Macquariella* and from all other littorinids by its very depressed spire, deep sutures and by its wide umbilicus. The large accessory lobe on the penis is unlike the simple penis of the type species of *Macquariella* and *Laevilitorina*, and the radula is intermediate in character between that of *Macquariella* and *Laevilitorina*. The radular characters given by Powell (1951) for the other generic and subgeneric groups recognised by him for the antarctic and subantarctic littorinids all differ appreciably from those of the new genus.

Rufolacuna brunensis (Beddome 1883)

Text Figs. 1-3, 12; Pl. 1, Fig. 2; Pl. 2, Fig. 9

Cyclostrema brunensis Beddome 1883: 168; Tate & May, 1901: 397, fig. 9; Pritchard & Gatliff, 1902: 99.

Skenea (?) *brunensis* (sic); Tate, 1899: 224.

Zalipais brunense; May, 1921: 43; May, 1923: pl. 20, fig. 22; Cotton, 1959: 237, fig. 159.

Skenella brunensis (sic); Gatliff & Gabriel, 1922: 146.

Shell: Minute, depressed-helicoidal, uniform dark reddish-brown, broadly umbilicate. Protoconch of 1 1/2 whorls, first 1/2 whorl rather large; teleoconch of 2 1/4 convex whorls; sutures deep. Surface smooth, rather dull, axial growth lines sometimes prominent, especially in umbilicus, and faint spiral scratches sometimes present. Inner lip sometimes partially separated from parietal area, with a thin edge but thickened within, posterior corner subangled, slightly advanced. Outer lip thin, simple, evenly convex, thickened slightly internally in anterior section (text Figs. 1-3).

Dimensions: Length 1.00 mm, diameter 1.75 mm (from original description)
1.24 mm 1.86 mm (figured specimen)

Operculum: Simple, smooth, of about 3 whorls, the nucleus slightly abcentric (Pl. 2, Fig. 9).

Radula: Each central tooth with narrow "neck" and small cutting edge having 1 large median cusp and 1 small lateral cusp on either side. Lateral teeth each with 3 inner cusps, 1 primary and 1 outer cusp; cutting edge of moderate width and about equal in width to those of inner marginal teeth which have the same number and configuration of cusps. Outer marginal with about 7 small, equal sized cusps (Pl. 1, Fig. 2). Radular sac long, spiral, of about 5 coils.

Head-foot: Tentacles, snout and foot all appear to be similar to those of *Macquariella kingensis*. Snout and dorsal foot dark grey, sole and tentacles white.

Penis: Rather large, penial duct appears to be enclosed along entire length. A long, simple appendage arises from the outer proximal end and is a little shorter than the total length of the penis. Both penis and appendage oval in section (preserved specimens from Fortescue Bay) (text Fig. 12).

Type: Three syntypes, TM (E305/7646) (one of these has been figured by Tate & May, 1901).

Type Locality: Cloudy Bay Lagoon, South Bruny Island, Tasmania.

Material Examined: Syntypes (TM); "Tasmania," pres. C. E. Beddome (AM); Derwent River Estuary, Tasmania (AM); Fortescue Bay, east side of Tasman Peninsula, southeast Tasmania, on littoral algae, coll. A. J. Dartnall, 1968 (TM); Eagle Hawk Neck, Tasmania (AM); Western Port Bay, Victoria (AM); 600 m off Middle Point, near Cape Northumberland, South Australia, 6 m, on algae, coll. S. A. Shepherd, 1974 (AM).

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BRIEF COMMUNICATIONS

AN IMPROVED RELAXING TECHNIQUE FOR MOLLUSKS USING PENTOBARBITAL.⁽¹⁾ — Since van der Schalie (1953) introduced nembutal for relaxing freshwater snails prior to fixation and preservation, this barbituric acid derivate has been widely used wherever malacological techniques are applied. Runham *et al.* (1965), in their review of narcotizing methods, pointed out that nembutal is most preferable in use with almost any group of mollusks, and van Aardt (1971) contributed to the understanding of its mode of action.

In the early 1960's, when nembutal was not easily obtained in all countries, the malacologist and pharmacist Dr. Werner Bolling, Bamberg, suggested that nembutal be prepared from sodium hydroxide and pentobarbital, which was then available. Since first attempts to use pentobarbital itself yielded good results, this chemical has been used from that time, and the experiences of 12 years of almost daily use are here reported.

Pentobarbital is the acid of which nembutal is the sodium salt. While nembutal easily dissolves in water, pentobarbital does not. It is a white, amorphous powder which floats on water and tends to sublime. Initially, some grains were put onto the surface of the water containing the mollusks, and the jar was covered (Meier-Brook, 1970: 76). This method worked well for several years, but it was still unsatisfactory because of a certain loss of substance by sublimation and a delay in effectiveness due to the relatively slight water contact. During the last years the method has been modified as follows: an amount of water 2 or more times the volume of the animals is mixed in a tube with some grains of the powder before the animals are added. A brief shaking results in a finer dispersion of the powder which, to a certain extent, sticks to the bottom and walls of the tube and later to the shells as well. The dissolution and diffusion of pentobarbital is so slow that, during the first minutes, the animals are apparently not affected: they creep around until their movements grow slower and slower. The adequate amount of pentobarbital required for total relaxation is found after a short time of experience. Even a tiny amount is sufficient provided it is well dispersed. If no grains are visible before the animals are ready for fixation, some more powder must be added; the best way is to add a little water which has previously been shaken with pentobarbital.

The relaxation results in a more or less complete extension of the head-foot complex in snails or of the foot in clams. When the animals no longer react to a stimulus with a needle or a pointed forceps, they are fixed in the usual ways. Formalin (4%), Bouin's fluid, etc., are preferable to alcohol, since in alcohol the molluscan tissues tend to shrink, often causing a partial withdrawal into the shells. When the shells are required in intact condition, the formalin should be well washed out after 1/2 or 1 hour, and the animals should be transferred to 70% ethanol.

The time needed for relaxation varies from group to group and is, generally speaking, shorter for smaller animals; basommatophoran snails are relaxed sooner than prosobranchs. Approximate data for some representatives of freshwater mollusks are listed in Table 1. As the figures indicate, bithyniid species require a considerably longer time than other species (data have been obtained for 4 species of the genus *Bithynia*, viz. *tentaculata*, *leachi*, *manchourica* and *misella*). Often the snails lay inactive on the bottom with their

TABLE 1. Examples of relaxation times in pentobarbital suspensions at 22-24°C prior to fixation with cold formalin (as to the use of hot formalin, compare text).

Mollusk	Relaxation time
Basommatophora:	
<i>Lymnaea (Radix) peregra ovata</i>	5 - 10 hours
<i>L. (Stagnicola) turricula</i>	1 1/2 days
<i>Planorbis</i> spp.	1 - 1 1/2 days
<i>Gyraulus</i> spp.	1 - 1 1/2 days
<i>Biomphalaria glabrata</i>	1 - 2 days
<i>Aplexa hypnorum</i>	1 day
Prosobranchia:	
<i>Bithynia</i> spp.	1 - 2 1/2 days*
<i>Valvata cristata</i>	20 - 24 hours
Lamellibranchiata:	
<i>Pisidium</i> spp.	1/2 - 1 1/2 days

* Sometimes a 2nd attempt is necessary after reactivation in clean water (compare text).

pentobarbital is almost impossible, even if the substance is added in excess. The extremely low (and slow) solubility of pentobarbital has the great advantage of raising the concentration gradually, and thus avoiding a shock in the animals, as may occur with nembutal in high dosages.

The effects of different dosing in the 2 relaxing agents were examined in a series of experiments in which mature planorbis snails of the same stock were exposed to from 2.5 to 40 mg of the substances, which were added to 10 ml of dechlorinated tap water. For the nembutal experiments, the respective amounts of a stock solution of Nembutal Abbott containing 50 mg/ml were diluted to 10 ml; for those with pentobarbital, 2 series of preparations were made as described above. To the 1st series the snails were added within 5 minutes after the addition of the substance; to the 2nd series they were added not before 2 1/2 hours, so that in the meantime the chemical could diffuse into the water.

The results (Table 2) indicate that pentobarbital can be used with good success in a considerably wider range of concentrations than nembutal, which should be applied in concentrations between 0.05 and 0.1% (data in boxes). Moreover, the results with pentobarbital added to the water 2 1/2 hours before use show some similarity with those in the nembutal series; this suggests that the particularly sparing action of pentobarbital on the snails is due to its low speed of dissolution and diffusion rather than to a mode of action basically different from that of nembutal. Pentobarbital can therefore be recommended as a very gentle and practicable relaxing agent for mollusks.

Summary. Among relaxing agents for mollusks, pentobarbital shows a mode of action similar to nembutal, but is more gentle and practicable due to its low solubility in water. It is dispersed in water in concentrations of 5 or more mg/10 ml before the mollusks are added. Accurate dosing is unnecessary, since even excess amounts of the chemical exert a sparing effect on the animals, provided the relaxing solution is prepared immediately before use.

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A COMPARISON OF TWO METHODS FOR ESTIMATING THE WEIGHT OF INORGANIC MATERIALS IN MOLLUSCS.⁽¹⁾—Ecologists have long recognized that in the computation of biomass and productivity, shells, bones and other relatively indigestible structures represent a portion of the biomass distinct from other tissues. The ecological significance is that the energy required by the organism to form these structures is not available to a predator. That is, such indigestible and often uneaten materials represent yet another loss of energy within a given trophic level that is not passed further up the trophic series (thus often termed "non-trophic growth"). Certain physiological measurements (such as respiration) are often expressed in terms of ash-free dry weight. For these reasons, many ecological studies exclude inorganic materials either by removing them from the computations (e.g., ash-free dry weight) or by using methods which determine carbon content or calorific value, which in theory are influenced only by the soft tissues (see Golley, 1961, for a discussion of ash and calorific value). This is especially important for organisms such as molluscs where the weight of the shell is often considerably greater than the dry weight of the tissues.

Two methods have been used to determine the inorganic content of shelled animals. Perhaps more widespread is the "ash method," where the tissues are removed by burning (leaving ash = inorganic material); various "acid methods," where the shell is removed by decalcification in a dilute mineral acid, have also been used. This study was an attempt to compare these methods and to briefly evaluate their differences using 2 species of snails.

Materials and methods. All of the animals involved in this study were adult freshwater pulmonates from 2 populations in southeastern Michigan. *Physa gyrina* Say (Basommatophora: Physidae) was collected from a small pond in Stony Creek Metropolitan Park (Macomb County, 42°44'09"N, 83°04'48"W), while *Helisoma anceps* (Menke) (Basommatophora: Planorbidae) was collected from Bald Mountain Lake (Oakland County, 42°44'58"N, 83°12'47"W). Both population sites are shallow, lentic man-made freshwater environments with detritus-covered mud bottoms and dense growths of littoral vegetation from which the snails were collected. The 2 population sites were similar in terms of physico-chemical characteristics. For the *Physa* site, mean summer pH = 8.3, conductivity = 270 micromhos and calcium concentration = 154 mg CaCO₃/liter; for the *Helisoma* site, mean annual pH = 7.7, conductivity = 314 micromhos and calcium concentration = 156 mg CaCO₃/liter.

Animals to be used in this study were fixed in 12% neutral formalin in the field, brought to the lab and stored. Prior to analysis, each snail was rinsed in tap water and, if necessary, cleaned of any heavy algal incrustations.

The methods which follow have been widely used in the past and, for the most part, differ only in certain details from previous accounts such as Richards & Richards, 1965 (on decalcification); Grove, Jones & Mathews, 1961 (on ashing).

Ash method. Ten adults of known shell length (for *Physa gyrina*) or maximum diameter (for *Helisoma anceps*) and known dry weight (dried to a constant weight at 105°C) were placed in unglazed 15 ml rose porcelain crucibles (Coors #32001). The snails were then ashed at 475–500°C for 50 minutes. It was necessary to place small steel covers on the crucibles since initial rapid heating of the dry snails caused "explosive" differential expansion. After cooling in a desiccator to room temperature, the crucible plus ash was weighed. The ash (largely CaCO₃ of the shell) was then placed in 40 ml of 3% nitric acid until decalcification was complete (all evolution of gas had ceased) leaving what is termed here, the residue (composed largely of sand grains and diatom frustules). The residue was then transferred by suction filtration to filter paper (Whatman #1) of known dry weight. After drying, these filter papers plus residue were weighed and the dry weight of the residue obtained by subtraction. In this way ash which is not CaCO₃ (i.e., the residue) could be estimated.

Acid method. Ten measured and weighed adults (as in the ash method) were placed in 40 ml of 3% nitric acid until decalcification was complete. Decalcification of dry, intact animals (as opposed to "ash") is relatively slow (2–3 hours) and caution was exercised to insure that all of the shell (especially the columella) was completely dissolved. The tissues which remained were then dried at 105°C, weighed and transferred to crucibles for ashing. The weight loss after decalcification was taken as equal to the weight of CaCO₃ in the shell. The dry weight of what remained after ashing the decalcified tissues was again the residue.

Results. Table 1 summarizes the results of the 2 methods when applied to *Physa gyrina* and to *Helisoma anceps*. An attempt was made to achieve nearly equal mean total dry weights (shell plus tissues) to enhance the strength of the comparisons. There was a high correlation between total dry weight and CaCO₃ content ($r = 0.9885$ for *P. gyrina* and 0.9968 for *H. anceps*) but a considerably lower correlation between maximum shell dimension and CaCO₃ content ($r = 0.8886$ for *P. gyrina* and 0.9023 for *H. anceps*).

As used in Table 1 the term "ash" has a somewhat different meaning depending to which method it refers. Strictly speaking, ash is the "weight of sample remaining after ashing" for the ash method and "weight loss due to decalcification" for the acid method. This difference, while real, is sufficiently small so that comparisons between the 2 methods based on the assumption that ash is roughly equivalent to CaCO₃ content show no significant differences (Table 2). It can be seen in Table 1 that the relationship of calcium to the tissues is quite different between the species, but not within a species, when the 2 methods are compared. For every mg of tissue in *Physa gyrina* there is an approximately equal weight of calcium, but in *Helisoma anceps* there is over twice the weight of calcium for every mg of tissue. In terms of residue as a percentage of "ash," clearly *P. gyrina* had a greater fraction of its ash as residue than did *H. anceps*. Differences between the methods are smaller than differences between species and are not so readily seen by inspection of means and measures of variation.

TABLE 1. Summary of basic data for *Physa gyrina* and *Helisoma anceps* using the ash and the acid methods. In all cases the computations are based on data from 10 individuals (i.e., N = 10). 95% C.I. = ninety-five percent confidence interval.

Species	Method	Mean maximum dimension (mm)	Mean whole dry weight (mg)	Mean "ash" (mg)	mg Ca/mg tissue dry weight			Mean residue (mg)	mg residue X 100/mg "ash"*		
					mean	S.D.	95% C.I.		mean	S.D.	95% C.I.
<i>P. gyrina</i>	ash	17.2	110.5	84.3	0.971	0.2305	0.1429	3.29	4.011	0.8371	0.5188
<i>P. gyrina</i>	acid	17.1	120.2	86.9	1.034	0.2858	0.1771	3.07	3.768	1.1759	0.7288
<i>H. anceps</i>	ash	11.3	110.6	92.6	2.054	0.0922	0.1191	1.34	1.507	0.9017	0.5589
<i>H. anceps</i>	acid	11.2	114.0	95.8	2.105	0.3223	0.1997	2.24	2.380	0.4858	0.3011

*Regarded here as equivalent to CaCO_3 content. See text for explanation.

In Table 2 are presented comparisons of the 2 methods within each species using the t-test. In terms of mg Ca, mg tissue dry weight there was no significant difference. No difference was found for mg residue/mg "ash" in *Physa gyrina* but was for *Helisoma anceps* ($P < 0.05$). Large and highly significant differences occurred between the 2 species using either method for both mg Ca, mg tissue dry weight and mg residue/mg ash.

TABLE 2. Comparison of mean calcium content per tissue dry weight and mean residue content of the ash as determined by the ash and acid methods for both *Physa gyrina* and *Helisoma anceps* using the t-test. P values indicate the significance probabilities and n.s. is "not significant" (i.e., $P > 0.05$).

Comparison	Significance probability	
	mg Ca/mg tissue dry weight	mg residue/mg ash
<i>P. gyrina</i> ASH to <i>P. gyrina</i> ACID	n.s.	n.s.
<i>H. anceps</i> ASH to <i>H. anceps</i> ACID	n.s.	$P < 0.05$
<i>P. gyrina</i> ASH to <i>H. anceps</i> ASH	$P < 0.001$	$P < 0.001$
<i>P. gyrina</i> ACID to <i>H. anceps</i> ACID	$P < 0.001$	$P < 0.01$

Discussion. Several reports in the literature have used gravimetric methods to determine ash content in gastropods enabling biomass or productivity figures to be expressed in ash-free or shell-less terms (e.g., Gillespie, 1969; Avolizi, 1970; Burky, 1971; Eckblad, 1971; Mason, 1971; Hunter, 1975a; McMahon, 1975). Other studies have dealt specifically with the calcium content of mollusc shells generally using decalcification as a means to obtain CaCO_3 content (Russell Hunter, Apley, Burky & Meadows, 1967; Russell-Hunter, Burky & Hunter, 1970; Nickerson, 1972; Hunter, 1975b).

The inorganic fraction of whole snails can be thought of as having 4 components (in approximate order of decreasing quantity): 1) shell CaCO_3 ; 2) inorganic gut content; 3) CaCO_3 in the tissues; and 4) other tissue salts. The ash method is a measure of all 4 components while the acid method is a measure of shell CaCO_3 only. Therefore, in theory, the ash weight should be greater than the weight loss upon decalcification. In practice, given the accuracy of measurement and the variation in these components between individuals, these 2 methods do not give significantly different results, at least for adult *Physa gyrina* and *Helisoma anceps*. This is also the case for another freshwater pulmonate, *Lymnaea palustris* (Hunter, unpublished). It is interesting to note that the methods do not yield the same results for residue as a percentage of ash for *H. anceps* but do for *P. gyrina*. This may be due to interspecific differences in weight of gut contents relative to total ash. Residue, whether determined by the ash or by the acid method, is both in theory and in practice very nearly the same (a result of exposure to ashing temperatures as well as to acid in either procedure). In the determination of "ash" by the acid method the gut contents escape detection. Thus residue as a percentage of ash is small when computed by the ash method but is larger when computed by the acid method (because $\text{ash} > \text{CaCO}_3$). Thus quantitative interspecific differences in relative gut contents (relative to whole animal ash) can result in differences between the 2 methods.

Differences between species in the relationship of calcium to tissue are likely to be the result of one or more of the following: population factors (genetic differences between populations), age factors (changes

during growth), environmental factors (i.e., CaCO_3 concentration in environmental water), and physiological factors ("de-growth" and parasitization). The influence of some of these factors on the Ca/tissue ratio is currently under study in our laboratory. The differences between *Physa gyrina* and *Helisoma anceps* using either method are not surprising. Even within species, differences in Ca/tissue are often large and, in the 2 freshwater pulmonates studied thus far, they are due to population factors (see Russell Hunter et al., 1967; Hunter, 1975b).

While the results should be applied to other species with caution, it would appear that, at least for certain species, the ash and acid methods give essentially identical results for the estimation of either total ash or CaCO_3 content of whole animals.

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IMMUNOLOGICAL REACTIONS OF FOOT MUSCLE PROTEINS OF FIVE SPECIES OF CYCLOPHORIDAE (GASTROPODA: MESOGASTROPODA) FROM SOUTH INDIA. (1, 2) — Immunology can be used to advantage in studying the relationships between different taxa, and the value of immunological methods in molluscan systematics has been well documented by Burch (1967a, b, 1968), Burch & Lindsay (1966, 1967, 1969, 1970, 1971), Burch & Hadžišće (1974) and Davis (1968a, b, 1971). The objective of the present study was to use an immunological method to study the relationships between 5 species of the prosobranch snail family Cyclophoridae in South India.

The species studied were *Cyclophorus jerdoni* (Benson), *Micraulax scabra* Theobald, *Pterocyclus bilabiatatus* (Sowerby), *Theobaldius ravidus* (Benson) and *T. shiplayi* (Pfeiffer).⁽³⁾ Large numbers of adult snails of each of the 5 cyclophorid species were collected from Alagarkoil, Madurai District, Tamilnadu State, India. The preparation of antigens and antisera followed the methods adopted by Davis (1967) and Burch & Lindsay (1970). In setting up the immunodiffusion tests, antigens were prepared by pooling foot muscle tissues from 5-7 snails and homogenizing 0.15 g (wet weight blotted tissue) in 1.0 ml of physiological saline. The procedure for setting up the micro-Ouchterlony immunodiffusion tests is shown in Fig. 1. Fig. 2 shows the interpretation of the precipitin bands.

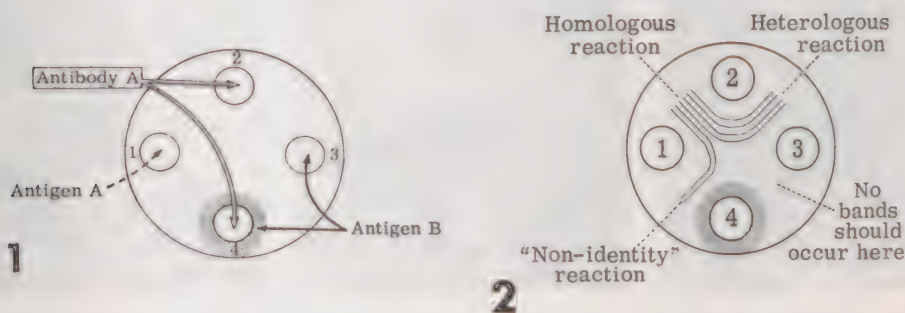


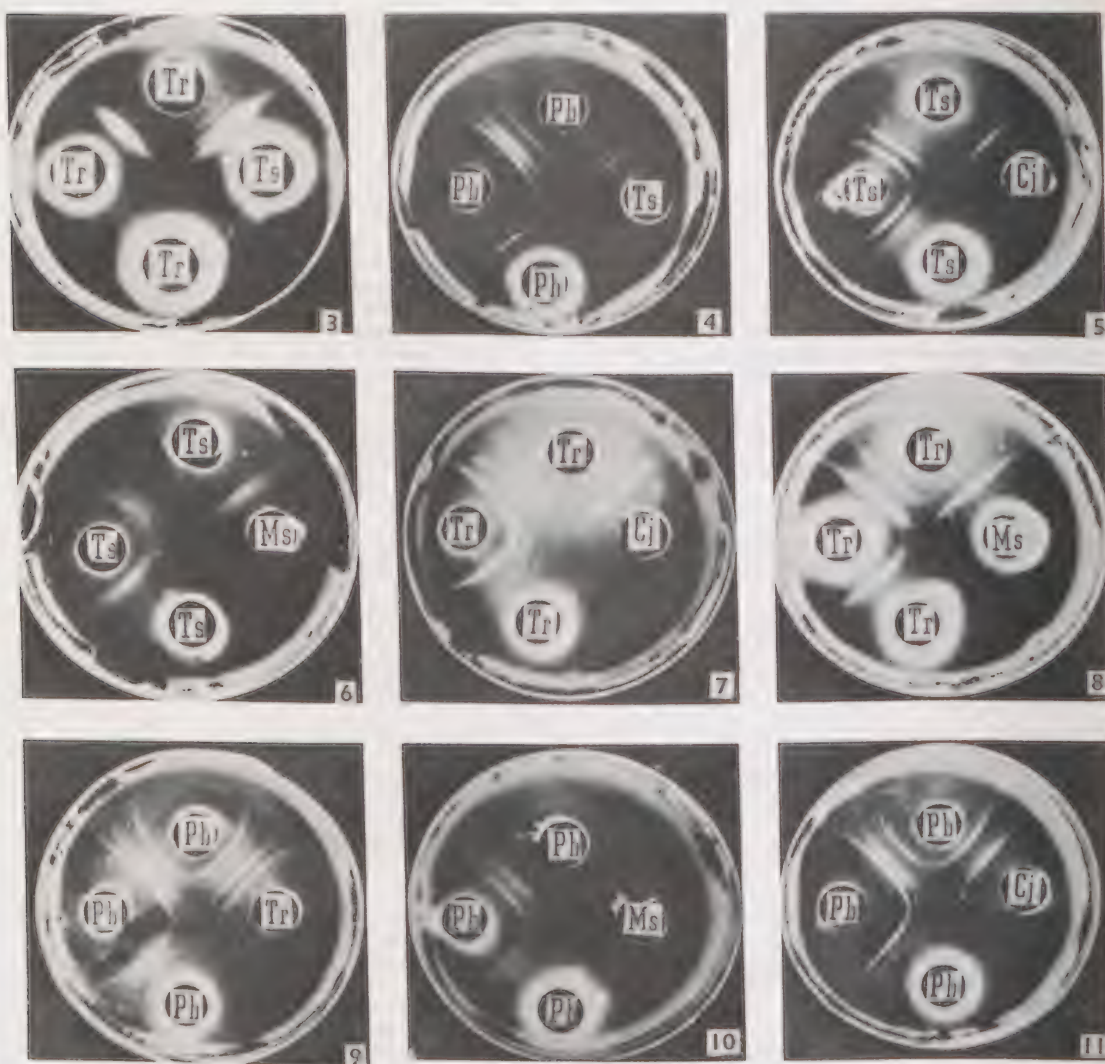
FIG. 1. Procedure for filling the wells with antigens and antisera in the micro-Ouchterlony double diffusion agar gel tests. Preabsorbed antigen is around well 4. Excess antigen for the preabsorption was removed before antiserum was placed in well 4. (From Burch & Lindsay, 1971.)

FIG. 2. Precipitation reactions of homologous proteins between the antibody and a heterologous antigen, i.e., from a different species. (From Burch & Lindsay, 1970.)

Photographs of the various micro-Ouchterlony plates are shown in Figs. 3-11. In each plate, the preabsorption well is at the bottom, antisera were put in the top and bottom wells, and the "identity" (absence of any band) or "non-identity" (presence of 1 or more bands) reactions occurred in the bottom left area between the left-hand and bottom wells.

In only the tests between *Theobaldius ravidus* and *T. shiplayi* was there an absence of precipitin bands between wells 1 and 4, indicating an "identity" reaction (Fig. 3). In all other tests, 1 or more "non-identity" precipitin bands occurred in the region between wells 1 and 4. As pointed out by Burch & Lindsay (1971), the absence of precipitin bands in this region indicates that the phylogenetic divergence between the taxa in question has not yet proceeded to a stage where new kinds of foot muscle proteins have evolved, i.e., it can be presumed that the 2 species are closely related. However, since "non-identity" precipitin bands developed when either of the 2 *Theobaldius* species were tested against one of the other 3 species, foot muscle proteins that do not occur in either *Theobaldius* species are present in the other 3 cyclophorid species (each of which is placed in a different genus on morphological grounds). Additionally, the 3 species - *Cyclophorus jerdoni*, *Micraulax scabra* and *Pterocyclus bilabiatatus* - each has foot muscle proteins which do not occur in the others (i.e., in their taxonomic divergence, each has evolved at least 1 specifically different foot muscle protein, and in several cases (e.g., *T. shiplayi* [ab] when compared to *C. jerdoni* [ag] (Fig. 5); *T. shiplayi* [ab] when compared to *M. scabra* [ag] (Fig. 6); *P. bilabiatatus* [ab] when compared to *M. scabra* [ag] (Fig. 10)) have evolved at least 2 specifically distinct proteins, and in at least 1 case (*T. ravidus* [ab] when compared to *C. jerdoni* [ag] (Fig. 7)) has evolved at least 3 specifically distinct foot muscle proteins).

In regard to the heterologous precipitin reactions (in the region between wells 2 and 3) between species pairs, it might be mentioned that some variation in the number of observable bands was detected. In particular, 6 bands were observed in tests between *Pterocyclus bilabiatatus* antiserum and *Theobaldius ravidus* antigen, and 3, perhaps 4, were observed in tests between *P. bilabiatatus* antiserum and *T. shiplayi* antigen. On the other hand, few and weak heterologous precipitin reactions occurred between *T. shiplayi* antiserum and *Cyclophorus jerdoni* antigen, and between *P. bilabiatatus* antiserum and *Micraulax scabra* antigen. However, since reciprocal tests were not run, antibody titers were not determined, and immunoelectrophoretic separations were not made, little reliance can be placed on the numbers of observable heterologous precipitin bands for making assessments of phylogenetic relationships. That will have to await further studies.



FIGS. 3-11. Micro-Ouchterlony immunodiffusion tests of antisera and antigens between various pairs of cyclophorid species. See Figs. 1 and 2 for explanation of procedure of filling wells and for interpreting the precipitin bands. Cj = *Cyclophorus jerdoni*; Ms = *Micraulax scabra*; Pb = *Pterocyclus bilabiatus*; Tr = *Theobaldius ravidus*; Ts = *T. shiplayi*.

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(3) Voucher specimens have been deposited in the collections of the Zoological Survey of India, Calcutta.

NEW DISTRIBUTION RECORDS FOR THREE SPECIES OF FRESHWATER LIMPET (PULMONATA: ANCYLIDAE) FROM NORTH CENTRAL TEXAS. — Intensive collections of freshwater gastropods from 1972 through 1975 in North Central Texas have revealed the presence of 3 species of freshwater limpet, *Laevapex fuscus* (C. B. Adams), *Hebetancylus excentricus* (Morelet) and *Ferrissia fragilis* (Tryon), all of the basommatophoran family Ancyliidae.⁽¹⁾ Of these 3 species, *Hebetancylus excentricus* was the most commonly found freshwater limpet in the North Central Texas region. It usually occurs on limestone rocks in riffle and pool areas of fast flowing streams. It is also occasionally found on rocks and rooted shore vegetation (particularly the Southern Bulrush, *Scirpus californicus* Tule) in lakes and ponds. This preference for lotic habitats does not agree with the canal and roadside ditch habitats described for Florida populations of this species (Basch, 1963), but is very similar to the limestone stream habitats of the earliest reports of *H. excentricus* in the United States from Comal Creek, Comal County, Texas (Pilsbry, 1889) and Barton Creek, Travis County, Texas (Walker, 1903). Both of these sites lie south of the *H. excentricus* populations we are reporting.

Hebetancylus excentricus has a general Caribbean distribution and occurs in the continental United States. It has been reported from Florida and Georgia (Basch, 1963) and from South Central Texas in Hays, Kerr, Jackson, Mason, Victoria (Basch, 1963), Comal (Pilsbry, 1889) and Travis counties (Walker, 1903). It is of interest to report the occurrence of *H. excentricus* in the Brazos River drainage of Hood, Somervell and Palo Pinto counties and in the Trinity River drainage of Dallas and Tarrant counties in North Central Texas, a region more than 200 miles north of previous records for this species in Texas. In these counties, populations of *H. excentricus* have been located at the following sites: Mountain Creek Lake (32°43'00"N, 96°58'24"W), Turtle Creek (32°48'08"N, 96°48'35"W), White Rock Lake (32°49'56"N, 96°42'51"W), Bachman Branch (32°51'36"N, 96°50'56"W) and Ten Mile Creek (32°52'00"N, 96°48'10"W) in Dallas County; Lake Worth (32°49'23"N, 97°26'50"W), Kings Branch (32°45'28"N, 97°25'15"W), Indian Creek (32°44'28"N, 97°24'34"W), Lake Arlington (32°43'05"N, 97°11'35"W), the Clear Fork of the Trinity River (32°37'13"N, 97°31'44"W) and Little Bear Creek (32°52'00"N, 97°05'59"W) in Tarrant County; Paluxy River (32°13'49"N, 97°46'31"W), Wheeler's Branch (32°14'40"N, 97°44'42"W) and Squaw Creek (32°17'10"N, 97°45'10"W) in Somervell County; Strouds Creek (32°27'33"N, 97°49'39"W) in Hood County; and the Brazos River (32°49'16"N, 98°24'50"W) in Palo Pinto County. A further population of *H. excentricus* was found in a small pond in Buescher State Park, Bastrop County (30°02'42"N, 97°09'46"W) in the Colorado River drainage of Central Texas.

Laevapex fuscus, the North American "pond" limpet, is distributed throughout the United States and Southern Canada east of the Rocky Mountains in swamps, ponds, slow rivers and lakes (Basch, 1959, 1963; Clarke, 1973). In North Central Texas, specimens of *L. fuscus* were collected from standing water habitats on the bases on the Southern Bulrush, *Scirpus californicus*, in 1-3 feet of water. Large populations of *L. fuscus* were located at the following sites in the Trinity River drainage system: Mountain Creek Lake (32°43'00"N, 96°58'24"W) and White Rock Lake (32°49'56"N, 96°42'51"W) in Dallas County; and Lake Worth (32°49'23"N, 97°26'50"W) in Tarrant County, Texas. Similar habitats on macrophytic vegetation in lentic environments have been reported for more northern populations of *L. fuscus* (Basch, 1959, 1963; Clarke, 1973). A 4th population of *L. fuscus* was collected from limestone rocks in impounded portions of Turtle Creek (32°48'08"N, 96°48'35"W) in Dallas County, Texas, a habitat similar to that reported for *L. fuscus* in Central New York (McMahon, 1975).

A population of *Laevapex fuscus* was also found on the bases of macrophytic vegetation in Tule Lake (28°06'41"N, 97°25'00"W), a small pond in Welder Wildlife Refuge on the Aransas River drainage of Southeastern Texas. These populations are the 1st records of *L. fuscus* from Texas (Basch, 1963; La Rocque, 1968). The nearest previous record for *L. fuscus* was from Lake Oberlin in Bryan County, Oklahoma (Branson & Peters, 1964).

A 3rd species of freshwater limpet, *Ferrissia fragilis*, was found in only 1 locality in North Central Texas. It was collected in flowing water from limestone rocks and the bases of bulrushes in Jackson Branch (32°54'33"N, 96°43'39"W) in Dallas County. This species is widely distributed throughout the United States east of the Rocky Mountains, but has not been reported in Canada or Mexico (Basch, 1963; La Rocque, 1968; Clarke, 1973). *F. fragilis* appears to be rather rare in North Central Texas and has been previously reported in Texas only from the Rio Grande (Clapp, 1913).

It is probable that Texas populations of *Laevapex fuscus* and *Ferrissia fragilis* lie near the southern extents of these species in North America. *Hebetancylus excentricus* has a general Caribbean distribution with entries into North America through Florida and Texas (Basch, 1963); therefore, these North Texas populations lie near the probable northern extent of this species.

The 2 genera, *Hebetancylus* and *Laevapex*, appear to be closely related, showing several unique common characteristics which separate them from the other North American Ancyliidae (Basch, 1959, 1963). Basch (1963) has postulated that *Laevapex* is the more highly evolved of the 2 genera, having arisen from *Hebetancylus*. Although these 2 genera are similar morphologically, they show a distinct habitat separation where their ranges overlap in North Central Texas. *H. excentricus* is found primarily on rocks in fast flowing streams, while *L. fuscus* is restricted to standing water habitats on rooted vegetation, rocks and other hard substrata in lakes and the impounded back waters of slow flowing streams and rivers. Generally the North American ancyliids are found in river or stream habitats characterized by flowing water. The exploitation of standing water environments by *Laevapex* may have been a major factor in its evolutionary divergence from the more lotic *Hebetancylus*.

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(1) Voucher specimens have been deposited in the Museum of Zoology, The University of Michigan.

FIVE NEW SPECIES OF LAND SNAILS FROM THE EASTERN UNITED STATES. — Five previously undescribed species of North American stylommatophoran land snails are described below.

Polygyra delecta new species. (Figs. 1-4.) Description. Shell very low conoidal, snuff brown to pale tawny-olive; umbilicate, the umbilicus about 0.2-0.3 mm in diameter, expanded in the last whorl to about 20% of the diameter of the shell, umbilicus with a shallow furrow parallel to the umbilical suture; whorls 4.7-5.5, 1st 1.5 whorls smooth, next 2 whorls finely striate radially, becoming rib-striate above, the rib-striae becoming weaker on the base, last whorl with numerous very fine deciduous hairs above and with very fine but distinct spiral impressed lines below; periphery high and rounded, convex below; aperture ear-shaped, lip broadly reflected, pale brown, oblique, sinuous, usually appressed to the body whorl in the umbilical region; within the outer margin there is an immersed tooth, rather broad and rounded, the edge usually bearing a recurved, forward-projecting hook; on the basal margin there is a rather short, stout and somewhat entering tooth with a buttress on its outer end; parietal tooth V-shaped, its lower edge raised and its axial end turned into the aperture; the parietal callus may or may not be raised in front of the tooth, and it has a forward projecting lobe at the axial end.

Selected shell measurements and whorl counts: height 4.5 mm, diameter 7.5 mm, aperture height 3 mm, aperture width 3.2 mm, umbilicus diameter 1.6 mm, whorls 5.2 [holotype; 3 mi north-northwest of Raleigh, Levy Co., Florida, U.S.A.]; height 4.4 mm, diameter 8.3 mm, whorls 5.5 [near Rosewood, Levy Co., Florida, U.S.A.]; height 3.5 mm, diameter 5.7 mm, whorls 4.7 [5.4 mi north-northwest of Otter Creek, Levy Co., Florida, U.S.A.].

Distribution. *Florida.* Levy Co.: wet roadside, 3 mi north-northwest of Raleigh (Type Locality), holotype 170933/1 and paratypes 170934/7, Field Museum of Natural History (FMNH); other paratypes 40853, collection of the author. Other Levy Co. localities are: drift, culvert, 1.5 mi southwest of Rosewood; roadside, 0.5 mi northeast of Sumner; near Waccasassa River, 1.8 mi north-northwest of Gulf Hammock; wet roadside, 5.4 mi north-northwest of Otter Creek; and wet roadside, 2 mi southeast of Chiefland. Taylor



FIGS. 1-4. *Polygyra delecta* Hubricht, Holotype. [Scanning Electron Microscope photographs (Figs. 1-4, 11-15) by Dr. Alan Solem, courtesy of Field Museum of Natural History.]

Co.: wet roadside, 8 mi south of Perry. Sumter Co.: roadside, 1.4 mi east of Colman; roadside, junction of Fla. Hwy. 44 and Fla. Hwy. 468.

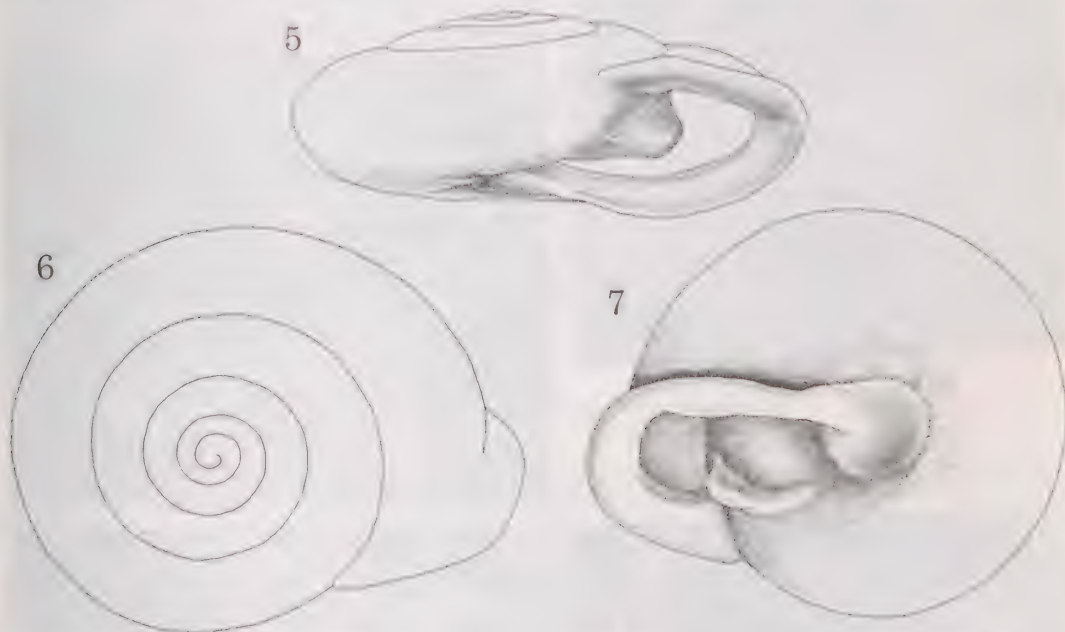
Remarks. *Polygyra delecta* is an extremely variable species. The front edge of the parietal callus may or may not be raised. The axial end of the lip and parietal callus is closely appressed to the preceding whorl in most specimens, but not in some specimens of the type lot. The hook on the outer lip tooth may or may not be present. The fine hairs are found on immature shells, but are usually lost on mature specimens. *P. delecta* is most closely related to *P. uvulifera* (Shuttleworth), differing from that species in its smaller size and the reduction in the relative size of the teeth, and in its darker color.

Mesodon panselenus new species. (Figs. 5-7.) **Description.** Shell strongly depressed, spire convex, pale brownish, glossy, imperforate, of about 5 whorls; 1st 2 whorls finely striate, later whorls rib-striate with engraved spiral lines over the shell; aperture oblique, ovate-lunate, constricted behind the lip; lip broadly reflected, white, with a weakly developed long blade-like lamina on the base; parietal callus thin, bearing a large, curved tooth, which is high near its outer end and does not reach the umbilical callus.

Height 8.3 mm, diameter 19.9 mm, 5.2 whorls. Holotype.

Distribution. *Virginia.* Buchanan Co.: low ground near creek, 2.2 mi southwest of Vansant (Type Locality), holotype 170940/1 FMNH; paratypes 42130, collection of the author. Wise Co.: wooded hillside, 2.2 mi west of St. Paul. Dickenson Co.: Grassy Creek Gorge, Breaks Interstate Park; wooded hillside, 2.5 mi south-east of Nora. *West Virginia.* Clay Co.: roadside dump, Scotford. Kanawha Co.: base of hill, 2 mi south-west of Hernshaw. Logan Co.: ravine, 2.4 mi southwest of Blair. McDowell Co.: 6 mi east of Iaeger.

Remarks. *Mesodon panselenus* is most closely related to *M. perigraptus* (Pilsbry) with which it has been confused. It differs from *M. perigraptus* in having a more depressed shell. Anatomically it differs in having a much shorter penis. *M. panselenus* is a species of southern West Virginia, and adjacent Kentucky and Virginia. I have not seen *M. perigraptus* north of Tennessee and North Carolina.



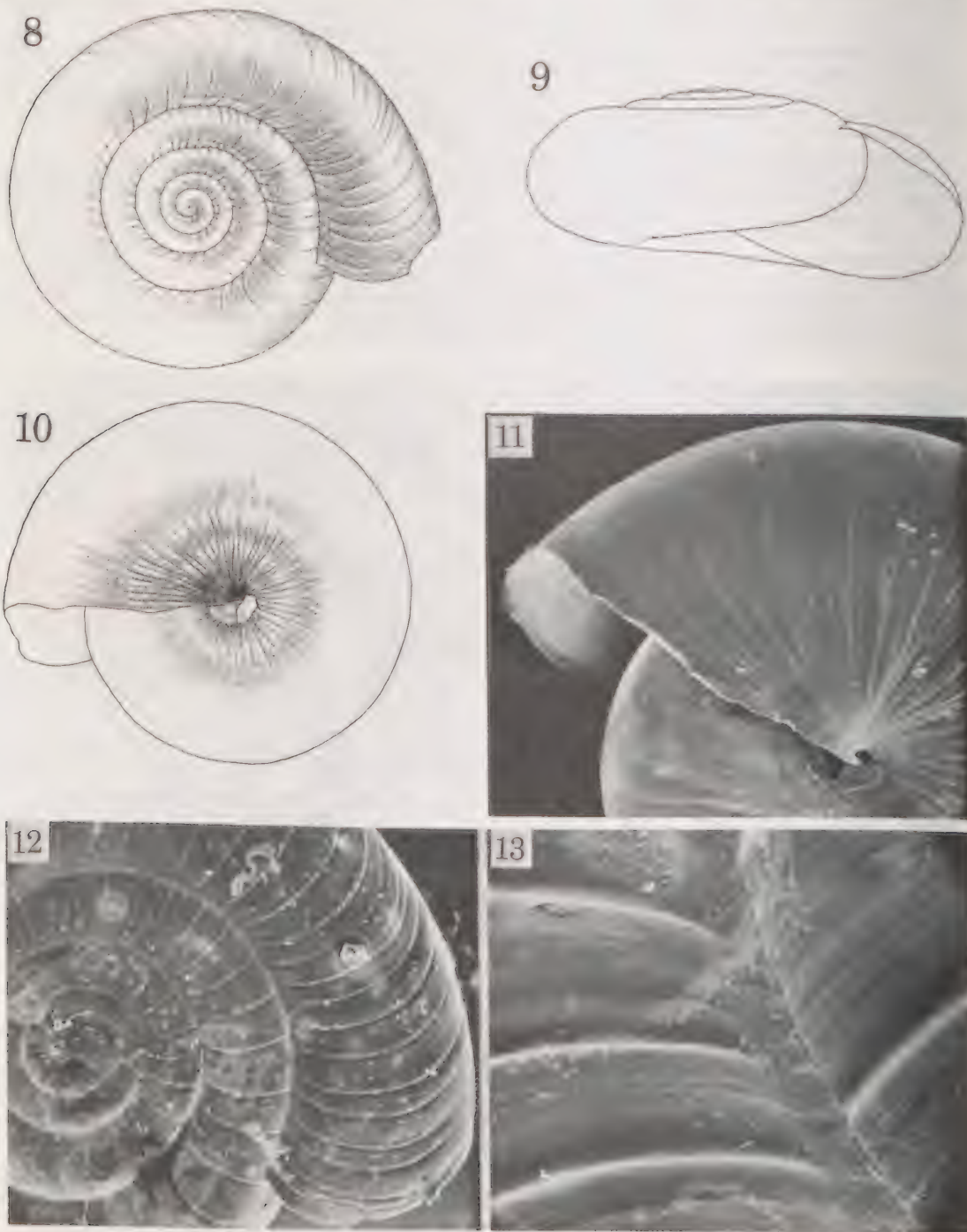
FIGS. 5-7. *Mesodon panselenus* Hubricht, Holotype. [Drawings by Elizabeth Liebman (Figs. 5-10, 16-18), courtesy of Field Museum of Natural History.]

Glyphyalinia picea new species. (Figs. 8-13.) **Description.** Shell medium in size, pale reddish-brown above, lighter below, subhyaline, shining; strongly depressed; sutures slightly impressed; whorls 5.5, regularly increasing; periphery well rounded; umbilicus rimate; aperture ovate-lunate; lip thin, simple; embryonic whorl smooth, later whorls with regular radial impressed lines which extend onto the base, and with numerous distinct spiral incised lines over the shell.

Height 3.0 mm, diameter 7.1 mm, aperture height 2.5 mm, aperture width 4.0 mm, 5.5 whorls. Holotype.

Distribution. *West Virginia.* Pendleton Co.: 4500 ft., east side of Spruce Knob (Type Locality), holotype 170939/1 FMNH; paratypes 40599, collection of the author. Randolph Co.: 3000 ft., maple flat, 1.4 mi north-east of Thornwood; 3900 ft., mountainside, 6.4 mi northeast of Thornwood. Preston Co.: mountainside, 0.5 mi south of Silver Lake. Pocahontas Co.: wooded hillside, 0.6 mi west of Durbin. *Maryland.* Garrett Co.: 3000 ft., Negro Mt., 3.2 mi west of Grantsville. *Virginia.* Highland Co.: base of hill, Denmark, 10 mi north-west of Lexington.

Remarks. *Glyphyalinia picea* is most closely related to *G. junaluskana* (Clench & Banks), from which it differs by its smaller size, more widely spaced radial lines and more distinct spiral sculpture. From *G. sculptilis* (Bland), with which it has been confused, the shell of *G. picea* differs by its more distinct spiral sculpture. *G. picea* differs from *G. sculptilis* anatomically by the absence of a penial appendix and in having the epiphallus distinctly bifurcate distally. The range of *G. picea* is allopatric to both *G. junaluskana* and *G. sculptilis*.



FIGS. 8-13. *Glyphyalinia picea* Hubricht, Holotype.

Paravitrea amicalola new species. (Figs. 14, 15) **Description.** Shell small, pale pinkish, subhyaline, shining; spire low, convex, with shallow sutures; whorls 6.5, slowly increasing, last quarter whorl slightly expanded in mature shells; periphery flattened in young shells, becoming well rounded when mature; umbilicus deep, well-like, contained about 3.5 times in the diameter of the shell; aperture lunate, oblique, about as wide as high, slightly flattened on the base; lip thin, simple; sculpture of irregularly spaced radial grooves and growth wrinkles, distinct above, but somewhat weaker on the base; in immature shells there is 1 (rarely 2) radial lamella about 1/4 whorl in from the aperture (in some shells this is replaced by a radial row of 3-4 teeth); mature shells are without lamellae or teeth.

Height 2.4 mm, diameter 4.1 mm, aperture diameter 1.7 mm, aperture width 1.8 mm, umbilicus diameter 0.7 mm, 6.5 whorls. Holotype.

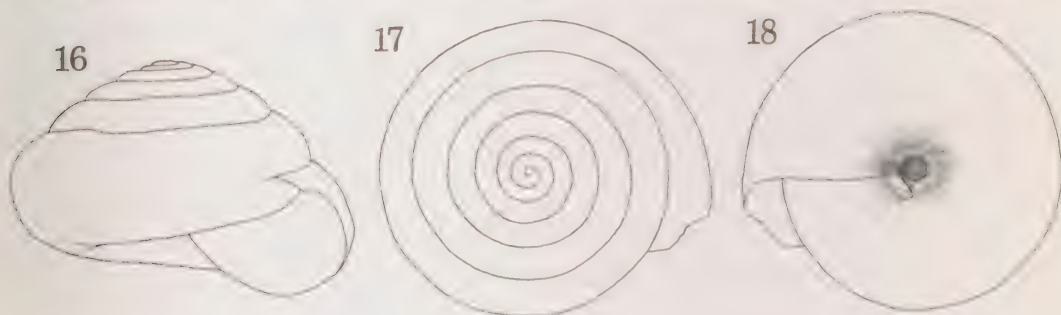
Distribution. Georgia. Dawson Co.: below Amicalola Falls (Type Locality), holotype 170937/1 and paratypes 170938/3 FMNH; other paratypes 25811, collection of the author; ridge, 1.5 mi southeast of Burnt Mt. Pickens Co.: ravine, 2 mi east of Jasper; wooded hillside, 2 mi northwest of Marble Hill; Mt. Oglethorpe.

Remarks. Despite the presence of a radial lamella, *Paravitrea amicalola* does not appear to be related to the *P. multidentata* group. It appears to be most closely related to *P. bidens* Hubricht, but differs from the latter in having a lamella or 3-4 teeth instead of a pair of teeth. Like most species of *Paravitrea*, *P. amicalola* breeds at any time that conditions are favorable, so that one finds several different age groups together. *P. bidens*, on the other hand, breeds only in the winter and the adults die off around the end of March, so all shells are about the same age.



FIGS. 14, 15. *Paravitrea amicalola* Hubricht, Holotype.

Ventridens arcellus new species. (Figs. 16-18.) **Description.** Shell low conoidal in shape, greenish-yellow to golden, shining, subtranslucent except for an opaque area behind the aperture formed by an internal callus; spire low, convexly-conic; sutures distinct; whorls 6.5-7.5, slowly increasing; periphery rounded; umbilicus deep and well-like, about 1 mm in diameter in mature shells, but sometimes smaller; base impressed around the umbilicus; aperture lunate, slightly oblique; lip thin and sharp; 1st 1.5 whorls smooth, later whorls with numerous, low, rounded, radial striae above the periphery, much smoother below; umbilical region with weakly developed spiral striae. There are no internal lamellae at any stage of growth.



FIGS. 16-18. *Ventridens arcellus* Hubricht, Holotype.

Height 9.2 mm, diameter 13.1 mm, aperture height 4.8 mm, aperture width 4.0 mm, 6.5 whorls. Holotype.

Height 9.6 mm, diameter 13.8 mm, 6.9 whorls. Paratype.

Height 11.1 mm, diameter 12.9 mm, 7.5 whorls. Paratype.

Distribution. Tennessee. Sevier Co.: 6600 ft., Clingmans Dome, Great Smoky Mountains National Park (Type Locality), holotype 170935/1 and paratypes 170936/9 FMNH; other paratypes A9162, collection of the author. *Ventridens arcellus* ranges from Randolph Co., West Virginia, southward in the mountains to Macon Co., North Carolina.

Remarks. *Ventridens arcellus* is most closely related to *V. acerra* (Lewis) and *V. demissus* (Binney). *V. acerra* is larger than *V. arcellus* and has a lower spire (an adult shell measured: height 12.9 mm, diameter 21.7 mm, 7.9 whorls), is not as excavated around the umbilicus, the color is usually more greenish and the shell is more opaque. *V. demissus* is much more depressed than *V. arcellus* and usually smaller. Both *V. acerra* and *V. demissus* are species of lower elevations, while *V. arcellus* is a species of mountain tops, usually occurring above 4000 ft.

The "holotype" of *Ventridens demissus* (U.S. National Museum cat. no. 38842) is a specimen of *V. arcellus*, but that specimen is so different from Binney's figure and description that it is an obvious case of mixed labels.

* * * *

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ABSTRACTS OF PAPERS

Presented at the

*SYMPOSIUM ON MOLLUSCA,
With Special Reference to the Sydney Area*

30-31 August 1975

Malacological Society of Australia
(Sydney Branch)
at The Australian Museum, Sydney

SYMPOSIUM ON MOLLUSCA

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Held at The Australian Museum, 30-31 August 1975

by the Malacological Society of Australia (Sydney Branch)

Organiser: W. F. Ponder

Chairman: F. W. D. Rost

This Symposium was hosted by the Department of Malacology of the Australian Museum and was supported in part by a financial contribution from the Trustees of the Australian Museum.

ABSTRACTS OF PAPERS

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AIMS AND SIGNIFICANCE OF ECOLOGICAL RESEARCH ON
INTERTIDAL GASTROPODS IN NEW SOUTH WALES

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Abstract

Intertidal gastropods in New South Wales are a sadly neglected group of species for experimental ecological study. Previous workers have almost exclusively confined themselves to a descriptive methodology. While this provides a background of observation and an overall view of the composition of the fauna of local shores, it has made no major contributions to our understanding of biological processes involved in maintenance of the life-styles of these animals.

Yet, gastropods are almost ideal organisms for ecological investigation in New South Wales. They are often widely distributed up and down the east coast of Australia, allowing comparative studies in different temperature zones. Several species occur in very high densities, allowing intensive sampling of local rock-platforms without danger of serious perturbation. They are easily marked, easily sampled using quadrats, and, in the absence of large intertidal algae, are easily recaptured for population studies.

This presentation described the major research projects currently in progress within the University of Sydney, to demonstrate the relationships between different types of ecological investigation. Many of these areas are being investigated in other institutions, and the purpose of the paper was twofold: (1) to delineate areas for future cooperation, and (2) to summarize progress on the major topics.

Reference was made to studies, at the level of populations, on reproductive cycles, larval life, recruitment, population densities, growth-rates, mortalities and food availability. Some processes of community structure and organisation were also discussed, with reference to mechanisms of coexistence, food competition, community stability and resilience, and recolonisation of denuded rock platforms.

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DISTRIBUTION AND RELATIONSHIPS OF THE OPISTHOBRANCHS OF NEW SOUTH WALES

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Melbourne, Australia*

Abstract

Biogeographically, the New South Wales coastline is within an overlap zone between tropical and warm temperate regions, with distribution of species controlled by sea-current and temperature. This results in a substantial tropical fauna on the northern coastline tapering off sharply to the south, and a much larger warm temperate fauna in the south tapering off less sharply to the north. The tropical fauna derives from the general Indo-West Pacific area, in particular the faunistically rich island complex to the north of Australia. The warm temperate fauna derives from several sources, reflecting past and present coastlines and sea temperatures. At the present time, the warm temperate opisthobranchs comprise 3 distinctive subgroups: (1) a large eurythermal subgroup extending along the whole coastline of southern Australia, (2) a small stenothermal (upper range of temperatures) subgroup centred on the northern half of New South Wales, and (3) a small stenothermal (lower range of temperatures) subgroup occurring in the southern half of New South Wales.

Endemism at the generic level is not apparent among the New South Wales opisthobranchs.

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THE OCCURRENCE OF *LYMNAEA* (*PSEUDOSUCCINEA*) *COLUMELLA* IN NEW SOUTH WALES

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Abstract

Lymnaea (*Pseudosuccinea*) *columella* is an intermediate host of the common liver fluke, *Fasciola hepatica*. This snail is native to the Western Hemisphere and is present in several countries of both North and South America, and it has been introduced into such places as South Africa, New Zealand and Hawaii. Following its recent recognition in Sydney, a survey was undertaken to determine the distribution of *L. (P.) columella* in New South Wales. In the Sydney, Newcastle, Wollongong, Moss Vale and Hampton areas, 168 sites were examined. Additionally, snails submitted by departmental field officers from 90 locations in coastal and tablelands areas of New South Wales were identified. The identifications of *L. (P.) columella* were confined to the Sydney area, with 9 out of 120 sites yielding this species. All the presently known locations are within 20 km of the Sydney General Post Office.

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THE TERRESTRIAL SLUG FAUNA OF SOUTHEASTERN AUSTRALIA

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Abstract

Slugs are gastropod molluscs in which the shell is either absent or reduced to a minute vestigial structure of little value as protection for the body. Eight families of terrestrial slugs occur in Australia, with 6 of these being found in southeastern Australia. Four of these families are introduced, several species of which are widespread and known as pests of crops and pasture. The introduced slugs belong to the families Milacidae, Limacidae, Arionidae and Testacellidae, the latter being a rare carnivorous group. The 2 families of native southeastern slugs, the Cystopeltidae and the Athoracophoridae, have more restricted distributions, limited mainly to native bush areas.

Field identification notes and distribution maps were given for each of the 10 species of slugs found in southeastern Australia. These 10 slugs are listed below.

Family MILACIDAE

Milax gagates (Draparnaud 1801)
(plus a possible variety)

Family LIMACIDAE

Deroceras caruanae (Pollonera 1891)
Deroceras reticulatum (Müller 1774)
Limax maximus Linnaeus 1758
Lehmannia (*Lehmannia*) *nyctelia* (Bourguignat 1861)
Lehmannia (*Limacus*) *flavus* (Linnaeus 1758)

Family ARIONIDAE

Arion intermedius Normand 1852
(possibly *Arion subfuscus* (Draparnaud 1805))

Family TESTACELLIDAE

Testacella haliotidea Draparnaud 1801

Family CYSTOPELTIDAE

Cystopelta petterdi Tate 1881
(possibly *Cystopelta bicolor* Pettard & Hedley 1909 and *Cystopelta purpurea* Davies 1912)

Family ATHORACOPHORIDAE

Triboniophorus graeffei Humbert 1863

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LATE QUATERNARY MOLLUSCA IN RELATION TO COASTAL BARRIER
STRATIGRAPHY IN NEW SOUTH WALES

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Abstract

During the last 3 years attempts have been made to further understand the morphology and stratigraphy of coastal sand barriers in New South Wales. Work has been concentrated in 3 areas: Moruya, Port Stephens-Myall Lakes and Evans Head. Stratigraphic investigations have involved drilling to depths of 40 m below sea level. Facies units have been documented by examination of sedimentary parameters and molluscan composition. Mollusc assemblages have assisted in the interpretation of environments of deposition. Radio-carbon dating of shell material has been used to clarify the age of sand barrier and estuarine deposits. Seven assemblages of Holocene age (last 10,000 years) have been recognised. These assemblages are associated with the following environments of deposition: (1) open ocean beach and upper nearshore, sandy; (2) open ocean lower nearshore, sandy; (3) tidal delta or nearshore adjacent to estuary mouth, sandy; (4) shell bioherm in estuary; (5) mud basin in estuary; (6) near shore estuarine, sand-mud; and (7) near shore estuarine, weedy sandbanks.

Drilling into sand deposits of the Inner Barrier has revealed a variety of molluscs and corals, the existence of which has not been documented in New South Wales before these investigations. Uranium-series dating shows these materials to vary in age from 140,000 to 120,000 years before present.

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SOME ASPECTS OF THE ECOLOGY OF *XENOSTROBUS SECURIS*

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Abstract

Distribution, growth rates, reproductive development and tolerances to variations in salinity, temperature and deoxygenation of *Xenostrobus securis* were studied.

Distribution was examined along the length of estuaries around Sydney (Hawkesbury to Port Hacking), and in the Tuggerah Lakes-Lake Macquarie region. Distribution tended to follow salinity reduction up an estuary - *Xenostrobus securis* can tolerate a wider range of salinities than other local mussels and can thus survive from almost fresh water to full seawater. Salinity, community and habitat determine final length and shape attained.

Population changes, growth rate and development were studied using mussels from the Munmorah Power Station intake canal, from March to September 1972. The species appears to have a life-cycle of 1 to 2 years and a maximum length of about 25 mm in this habitat. Gonad maturation begins in June-July in animals which settled the previous October. Spawning begins with an increase in water temperature in October and continues throughout summer, with a 2nd peak in about January. Environmental conditions may vary this pattern.

Xenostrobus securis is more resistant to deoxygenation at all temperatures than either *Mytilus edulis* or *Trichomya hirsuta*, the other common mussels of the Sydney region.

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THE INFLUENCE OF PREDATORS ON VICTORIAN ROCKY SHORE MOLLUSCS

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Abstract

The prey taken by the 3 main predators of Victorian rocky shore molluscs, *Pseudolabrus fucicola* (purple parrotfish), *P. tetricus* (blue nose parrotfish) and *Haematopus fuliginosus* (sooty oystercatcher) are recorded for the 1st time. The habitat and zonation patterns of a number of species of gastropods were discussed in relation to this predation.

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THE ROLE OF FOOD AVAILABILITY IN DETERMINING THE DEGREE OF SHELL COLOURATION AND BANDING IN *AUSTROCOCHLEA CONSTRICTA*

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Abstract

The shells of the common Australian intertidal gastropod *Austrocochlea constricta* (Lamarck) exhibit a wide variety of patterns of banding and colouration. A possible environmental link between food availability, banding and various population parameters was investigated. Six shores in the Sydney region were investigated, representing the range of habitats of the species. Qualitative and quantitative methods were used to determine the concentrations of chlorophyll pigments in the substratum of each shore. A preliminary investigation using thin layer chromatography showed that there were differences between shores in the type of algae present. Quantitative spectrophotometric determinations of the chlorophyll pigments in the substrata were then performed on all 6 shores. This measurement of the amounts of plant pigments present provides an estimate of food availability. There were significant differences in chlorophyll concentrations between shores.

The major pigment responsible for shell colouration was found to be Uroporphyrin 1. The concentrations of this pigment varied between localities and between shell types. A Uroporphyrin Index, relating wet weight/animal, density/quadrat, proportions of the population in different stripe classes and the concentrations of Uroporphyrin, was constructed for each shore. There was a highly significant linear relationship of regression of Uroporphyrin Index on total chlorophyll concentration. This provides evidence for a quantifiable effect of amount of available food on shell pigmentation; the mean concentration of pigment/gram of shell increases as the chlorophyll content of the substratum increases.

A series of caging experiments was performed to test for banding changes when animals were transferred from one locality to another. Banding pattern changes noted both from these experiments and from general observations support the hypothesis that food availability, rather than a genetical factor, determines the amount of pigmentation in the shells of *Austrocochlea constricta*.

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CHLOROPLAST "SYMBIOSIS" IN OPISTHOBRANCHS FROM NEW SOUTH WALES

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Abstract

Certain opisthobranchs are able to incorporate intact chloroplasts into the cells of their digestive glands; these chloroplasts may continue to fix carbon by photosynthesis for considerable periods in the animals. The physiology of such relationships and their occurrence and variations in local species was discussed.

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ELEMENTS OF THE AUSTRALIAN LAND AND FRESHWATER MOLLUSCAN FAUNA
AND THEIR RELATIONSHIPS TO OTHER FAUNAS

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Abstract

Australia has a large and in many respects unique land and freshwater mollusc fauna. The zoogeographic and phylogenetic relationships of many of these animals, especially to foreign pulmonate snail taxa, is not well understood, largely because of the rather scant attention these subjects have so far received. The most recent hypothesis regarding the relationships of Australian land snails has supposed that their peculiarities and affinities can be explained by successive waves of migrations of faunal elements from the north, i.e., from Southeast Asia, the Malay Archipelago, Indonesia and Papua New Guinea. According to this supposition, the more ancient or generalized elements have been pushed to the southern fringes, and a similar situation exists in Africa and South America -- the "more primitive" land snails occur in the Southern Hemisphere because they have been preserved in "southern refuge zones." Such north-to-south migrations have obviously occurred in the past, and there is a clear affinity of some Australian pulmonate faunal elements with those to the north. However, it is easier to explain the relationships that some of the Australian-New Zealand land and freshwater molluscan fauna have with southern Africa and South America by a southern distribution route, and it would seem that "continental drift" may have played a rather significant role in the distribution of pulmonate snails in the Southern Hemisphere. Now that so much information is being accumulated on geological aspects of plate tectonics, or movements of the earth's crust, it is time for a more detailed appraisal of the zoogeographic affinities of Australian pulmonate mollusc faunas.

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SPERM ULTRASTRUCTURE AND BIVALVE PHYLOGENY

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Abstract

In order to determine whether the morphology of spermatozoa of the Bivalvia could be correlated with the evolutionary history of this class, testes of a number of species were prepared for electron microscope examination and observed. Representatives of the Bivalvia included: species of the subclass Pteriomorpha, *Anadara trapezia*, *Anomia descripta* and *Mytilus edulis*; species of the subclass Heterodonta, *Fulvia tenuicostata*, *Mysella* sp. (a brooder of its young), *Notocorbula vicaria*, *Paphia scordalus*, *Tellina deltoidealis* (a brooder of its young) and a number of teredines (some species of which also brood their young); and a single species of the subclass Anamalodesmata, *Myodora brevis*.

The following observations of significance were made. Spermatozoa of *Anadara trapezia*, *Anomia descripta*, *Fulvia tenuicostata* and *Myodora brevis* contain acrosomes which do not have axial rods. Until this present work, it appeared that an axial rod was a feature of the acrosome of bivalve sperm. Furthermore, the acrosome in the sperm of *M. brevis* was found to be situated near the mitochondria of the mid-piece rather than capping the anterior end of the nucleus as in the vast proportion of spermatozoa found within the animal kingdom. The spermatozoa of *Mysella* sp. and *Tellina deltoidealis* were found to be elongated in comparison to other bivalve sperm. In the case of *Mysella* sp. the acrosomal granule was also found to be relatively small. The significance of this finding becomes apparent when it is correlated with the mode of rearing of the young of this species. Since it is a brooder, fertilization must take place in the mantle cavity, unlike that in most species of bivalves in which fertilization of the eggs takes place externally. Hence it is suggested that sperm structure in bivalves can be easily correlated with whether or not the species is a brooder.

Other conclusions reached are that sperm structure, especially within the subclass Pteriomorpha is not easily related to bivalve phylogeny, as the structure of the sperm varies so much among species. Since the lack of the presence of an axial rod has been found in 3 subclasses of the Bivalvia, it becomes apparent that sperm ultrastructure of species of all orders of the Bivalvia, especially the Nuculoida and Solemyoida, should be examined in order to obtain an accurate estimation of the range of variation of bivalve sperm morphology.

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CURRENT RESEARCH INTO THE BIOLOGY OF FARMING MUSSELS IN AUSTRALIA

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Abstract

The blue mussel *Mytilus edulis* is a bipolar species widely distributed through cold and temperate waters. The fact that it is a fast growing "weed" species of great reproductive capacity makes it particularly suitable for culture. During a 3-year programme, 12 experimental rafts have been operated between Port Stephens and Perth. It has been demonstrated that mussels can be successfully cultivated despite the problems of fouling floods and predation. Comparisons were made with the New Zealand mussel farming industry.

ASPECTS OF THE HOST-PARASITE RELATIONSHIP BETWEEN
VELACUMANTUS AUSTRALIS AND ITS TREMATODE PARASITES

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Abstract

In the Sydney region, *Velacumantus australis* is commonly infected with 7 species of trematode parasites, with infection rates of 60-70% in some populations. The relationship between these trematode species and their host is being studied in both natural and laboratory situations.

One of the aspects of this host-parasite system being investigated is the pathological effect of the trematodes on the snail host, particularly the damage to the digestive gland and gonad. In part, this involves the analysis of thin sections of the snail's digestive gland and gonad by the technique of stereology, which allows information on volumes and surface areas of tissue components and parasites to be derived from simple counting operations. This technique should be of value in other studies involving the use of thin sections, where quantitative data on tissues and their component cells is required.

THE DISTRIBUTION OF SEVERAL INTERTIDAL MOLLUSC SPECIES IN RELATION TO SYDNEY HARBOUR

B. W. Jenkins

University of New South Wales, Sydney, Australia

Abstract

The distributions of the gastropod molluscs *Cellanatra moserica*, *Nerita atramentosa*, *Littorina unifasciata*, *Austrocochlea constricta*, *Bembicium nanum*, *B. auratum*, *Morula marginalba*, *Ophicardelus ornatus* and *Salinator solida*, and the bivalves *Trichomya hirsuta*, *Xenostrobus securis*, *Lasaea australis* and *Saccostrea cucullata*, were investigated in the estuary system of Sydney Harbour. To complete an outline of the changing zonation marked by the dominant zoning organisms, the serpulid worm *Galeolaria caespitosa* and the coralline algae were included along with the several molluscs selected. The survey ranged from the coast outside the estuary to the tidal limits of Middle Harbour and the Parramatta, Lane Cove and Duck Rivers.

The results, besides providing information for plotting distributions, showed notable features of estuarine ecology. Horizontal distribution of the rocky shore marine-mesohaline species showed that those occurring in higher shore zones penetrated further into the estuary than species in lower zones. The bivalves *Trichomya hirsuta* and *Saccostrea cucullata* were widely marine-mesohaline, both occurring on the coast outside the estuary, developing as dominant zone organisms within the estuary (lower mid-littoral and infra-littoral zones respectively) and penetrating into regions of low salinity. *Lasaea australis* was solely marine, occurring on the coast outside the estuary and around the mouth of the outer harbour where siltation was receded and turbidity increased compared to conditions further in the estuary. The small mussel *Xenostrobus securis* was limnic-mesohaline, exhibiting a wide tolerance to sea water conditions. It existed from the tidal limits at the head of the estuary to areas where marine-mesohaline species occurred, which was the region displaying the greatest environmental changes throughout the estuary. *Salinator solida* and *Ophicardelus ornatus* were mesohaline and directly associated with mangrove and saltmarsh habitats. Substrata, particularly seawalls, directly influenced which intertidal organisms were present. Smooth surfaces mainly support sessile organisms and provide little protection for motile organisms. Explanations of changes in distribution and relationships between species were discussed in terms of various limiting factors: substratum, shore disturbance and dominant zoning organisms, as well as ranges of water temperature, salinity and dissolved oxygen content.

THE STUDY OF AUSTRALIAN MICRO-MOLLUSCA AND ITS APPLICATIONS

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Abstract

There is a very large fauna of minute molluscs in Australia, but the majority are very poorly known and many of them are undescribed. Several groups are abundant in intertidal habitats where they live mainly on algae or beneath stones. Qualitative field observations suggest that a sharp reduction in diversity and changes in species composition occur in disturbed or polluted areas. Such changes are currently monitored by information obtained from samples of large animals, but the collecting, sorting and storing of micro-molluscs is much less time-consuming and requires little working and storage space. The main problems yet to be resolved are standardisation and quantification of sampling methods and identification of material. The latter problem is the chief concern of the writer, and illustrated reviews and keys of the species in the important families occurring in the intertidal and shallow sublittoral zones are currently being produced.

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REPRODUCTIVE CYCLES OF SIX SPECIES OF LITTORINIDS IN THE SYDNEY AREA

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Abstract

The reproductive cycles of 4 species of littorinids from rock platforms and 2 species from mangroves of the Sydney region are being studied over a period of 15 months. Their reproductive cycles are discussed with regard to release of young at the time of maximum availability of phytoplankton. The reproductive strategies of the 6 species are not correlated directly with tidal zonation. Behavioural mechanisms in the form of lunar and tidal spawning periodicities must also be taken into account. The correlation of spawning with the period of maximum food availability for the larvae has been investigated by means of several experiments using temperature as the variable parameter. Ideas for further work on the ecology and behaviour of the 2 mangrove littorinids, together with some observations on the brooding of embryos by *Littorina scabra*, were presented.

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THE BIOLOGY OF *ANADARA TRAPEZIA* WITH PARTICULAR REFERENCE TO ITS HAEMOGLOBIN

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Abstract

Anadara trapezia is a bivalve mollusc which is a common inhabitant of the shallow benthic weed beds in the estuaries of the east coast of Australia. Its blood contains 2 intracellular haemoglobins, 1 of which is polymorphic. The polymorphic haemoglobin is controlled genetically by 1 pair of alleles. One allele is more common in populations in northern Australia, the other is more prevalent in southern populations. All populations are in Hardy-Weinberg equilibrium and a complex cline in haemoglobin gene frequencies occurs.

The polymorphic haemoglobins have been separated and their oxygen equilibrium curves (OEC) studied. It was found that the OEC of the northern form lies to the right of that of the southern form at 15, 20 and 25°C. The OEC of the heterozygote lies between those of the 2 homozygotes. Such a difference between the OECs is probably an important adaptation to life in the intertidal mud.

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RESPONSES OF SEVERAL GASTROPODS TO ENVIRONMENTAL STRESS:
ADENYLATE ENERGY CHARGE A SUITABLE INDICATOR?

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Abstract

Adenylyl energy charge (EC) may provide a tool which is useful in determining stress conditions quickly in estuarine organisms. Preliminary experiments which investigated the effect of salinity stress indicate that the EC in muscle tissue of *Pyrazus ebeninus* changes with a decrease in salinity.

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OYSTER DISEASES AND PARASITES IN AUSTRALIAN OYSTERS

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Abstract

The importance of the study of oyster diseases and parasites becomes clear when it is remembered that the oyster production of New South Wales alone has an annual value of about 9 1/2 million Australian dollars.

In the estuaries of the New South Wales mid- and south coast, a condition known as winter mortality causes great yearly losses to culturists. In the northern estuaries of New South Wales and in Queensland, oysters are killed each year in great numbers by a haplosporidan parasite, tentatively named QX¹. Oysters from the subtropical and tropical region of Australia are plagued by a larval tapeworm,² which is normally not lethal, but can cause great loss of condition of the oysters. Oysters from the Northern Territory have recently been found to harbour an ovarian parasite of unknown taxonomy, but this does not cause any apparent losses to the natural beds.

During the studies undertaken, the 1st true neoplastic growths in molluscs were discovered, which, although economically unimportant, are considered important in the research of tumours in lower animals.

¹It has since been identified as *Marteilia sydneyi* n. sp.

²*Tylocephalum*.

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RECORDINGS OF THE PHYSIOLOGICAL ACTIVITY OF MOLLUSCS IN THEIR NATURAL HABITATS

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Abstract

By the use of suitable techniques it is possible to record the heart activity of molluscs in their natural habitats. These techniques may be used to determine the activity patterns of individuals and also to determine activity patterns of populations.

Although such recordings allow a measure of the physiological activity of molluscs under environmental conditions, their value is to some extent dependent on a knowledge of the relationship between heart activity and other aspects of metabolism and behaviour. Such knowledge is fragmentary. Something is known of the general relationships between heart activity and valve activity (of bivalves), pumping activity (of bivalves), feeding and respiration, but the effects on heart activity of processes occurring at an organic, cellular or subcellular level are not understood.

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NOTES AND OBSERVATIONS ON THE MURICID GASTROPOD
CHICOREUS DENUDATUS IN SYDNEY HARBOUR

Neville Coleman

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Abstract

Observations were presented on feeding habits of *Chicoreus denudatus*, its egg laying procedures, habitat and substrate, an unusual relationship of the juvenile with the adult, lip growth observations and growth rate tagging experiments. A short summary of this mollusc's taxonomic history was given and ideas presented as to why the distinguishing features of the Sydney Harbour form is unreliable and therefore unworthy of subspecific rank.

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NEWS AND ANNOUNCEMENTS

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THE NETHERLANDS MALACOLOGICAL SOCIETY. — The year 1974 was marked by the 40th anniversary celebrations; the society was founded in 1934 and started publishing *Basteria*, its scientific journal, in 1936. Celebrations were conducted in the new auditorium of the Free University, Amsterdam. Over 150 participants (the highest number of people ever attending a meeting of the Society) attended 2 invited lectures (Prof. Lever on mollusc research in the famous mollusc-oriented Zoology Department of the Free University, and Mrs. Dr. Van Benthem Jutting on the history of the Society), 2 special exhibitions (Rijksmuseum, Amsterdam, on shells in art, and Zoological Museum, Amsterdam, on molluscs in general), an evening film session, and lunch and dinner.

Membership rose to 425 (total population of the Netherlands about 13 million), members participating in meetings, field trips and library facilities, while receiving 6 issues of the roneoed newsletter and a volume of *Basteria* per annum for the equivalent of approximately US\$ 10.00. A little atlas of fossil gastropods found on the beaches or obtained from surface beds was reprinted and sold well.

Address of the Honorary Secretary: Mr. J. G. B. Nieuwenhuis, Bentincklaan 37A, Rotterdam-3004, Holland.
— A. C. VAN BRUGGEN

FIFTH SOVIET MALACOLOGICAL MEETING. — Since 1961, All-Union Meetings on Molluscan Research by Soviet malacologists have been held every 3-4 years in the Zoological Institute of the U.S.S.R. Academy of Sciences in Leningrad. These forums have been organized by the Malacological Committee of the Scientific Council on "Biological Bases for the Use, Protection and Reconstruction of the Animal World." From 11-14 February 1975, the Fifth All-Union Meeting on Molluscan Research was held. The main objective of the Fifth Meeting was to sum up and discuss the further perspectives for mollusc studies and the results of the application of new research methods. One hundred and forty-three scientists from 36 cities and 55 institutions took part in the Meeting. Fifty-six reports were read, 22 in plenary sessions and the rest in 3 specialized sections on marine, continental and fossil molluscs.

Particularly interesting were reports on evolution and taxonomy of molluscs in general and on the several molluscan classes (e.g., "New data for construction of systematics of Bivalvia," O. A. Scarlato & Ya. I. Starobogotov; "On the systematics of euthyneuran gastropods," Yu. S. Minichev & Ya. I. Starobogotov; "Peculiarities of the structure of the excretory system of the Pulmonata in relation to subclass classification," A. A. Schileiko; etc.). The main conclusions of these reports were based on new original data of the authors and on critical review of the literature. A number of reports were devoted to the characteristics and zoogeographic analysis of malacofaunas of various territories and aquatoria which are not yet well studied (e.g., West Siberia, B. H. Hohansen & E. A. Novikov; drainage of Petchora, Ju. V. Leshko & L. N. Solovkina; Tonkin Bay, I. P. Zorina; Balkan halbinsel, I. M. Likharev; etc.). Reports containing new approaches to the problem of growth and production and problems of energetics in mollusc populations (A. N. Golikov, A. F. Alimov, V. H. Zolotarev, and others) attracted much attention. Discussion of these reports allowed coordination of methods and theoretical approaches to the analyses of results. A number of reports contained new information on life cycles and reproductive biology of molluscs, especially commercially important species, transmitters of helminths, and pests. Paleomalacologists delivered a number of reports devoted to the faunal changes at the end of the Mesozoic and the beginning of the Cenozoic, and to the importance of molluscs for the establishment of a demarcation line between these 2 epochs (O. V. Amitrov, V. M. Shimansky, H. H. Martinson, and others). New data on shell structure of Recent and fossil molluscs helped in making conclusions on evolution and taxonomy of these animals (I. S. Barskov, V. V. Drushitz, and others). Several reports (A. P. Brestkin, P. V. Matiokin, B. M. Logvinenko, and others) dealt with the results of the application of biochemical methods (e.g., disc-electrophoresis of proteins, specificity of cholinesterases) for solving problems of micro- and macrosystematics.

The reports presented at this Fifth Meeting and the discussions which followed indicate that interest towards molluscs continues strongly and their study is being expanded. At the final session a resolution, which contained directions for further investigations by Soviet malacologists, was discussed and adopted. The new officers of the Malacological Committee, which will convene the next Meeting in 1979, were elected.

Reports of the Fifth Soviet All-Union Meeting on Molluscan Research will be published in the near future.
— I. M. LIKHAREV, Chairman of the Malacological Committee

MALACOLOGICAL SYMPOSIUM, SYDNEY, AUSTRALIA. — A "Symposium on Mollusca, with Special Reference to the Sydney Area" was held at The Australian Museum in Sydney by the Malacological Society of Australia (Sydney Branch) on 30-31 August 1975. The Symposium, perhaps the largest malacological meeting ever held in the Southern Hemisphere, was organized by W. F. Ponder (The Australian Museum), chaired by F. W. D. Rost (University of New South Wales), and hosted by the Department of Malacology of The Australian Museum. Abstracts of the papers presented at the Symposium can be found on p 131-141 of this issue of *Malacological Review*.

MOLLUSCAN WORKSHOP, LIZARD ISLAND, NORTHERN GREAT BARRIER REEF, QUEENSLAND, AUSTRALIA. — A group of malacologists met to study tropical molluscs on a remote island in north Queensland during the first 2 weeks of December 1975. The location was The Australian Museum's Research Station at Lizard Island, which lies to the north of Cooktown, and the occasion was Australia's first Molluscan Workshop. Nine malacologists and several support personnel attended the Workshop and, despite unseasonably wet and windy weather, the participants were able to accomplish a considerable amount of work. It is hoped that a collected series of papers resulting from the Workshop will be published by early 1977.

The participants included C. M. Yonge (University of Edinburgh, Scotland, U.K.), Brian Morton (University of Hong Kong, Hong Kong), Clyde F. E. Roper (Smithsonian Institution, Washington, D.C., U.S.A.), B. R. Wilson and Shirley Slack-Smith (Western Australian Museum, Perth, Australia), Brian J. Smith (National Museum of Victoria, Melbourne, Australia), Robert Burn (Geelong, Victoria, Australia), J. B. Burch and Winston Ponder (The Australian Museum, Sydney, Australia). The Workshop was conceived and organised by Dr. Ponder with the help of the staff of the Department of Malacology at The Australian Museum.

The projects undertaken by the participants included studies on *Tridacna* (Yonge and Morton), the functional morphology of *Fimbria* (Morton), a survey of the land molluscs of Lizard Island and the neighbouring islands (Burch and Smith), miscellaneous chromosome studies (Burch), comparative studies of 2 species of Rhytididae (Smith), aspects of the anatomy of *Fossarius*, *Planaxis* and *Pyramidella* (Ponder), a survey of, and observations on, various cephalopods (Roper), a survey of the opisthobranch fauna (Burn), the comparative anatomy and ecology of oyster species (Slack-Smith), and the comparative anatomy and ecology of *Lithophaga* species (Wilson).

Support personnel assisting the malacologists were Phillip H. Colman, Ian Loch, Margaret S. Burch and Barbara Duckworth.

DEUTSCHEN MALAKOZOÖLOGISCHEN GESELLSCHAFT. — Einladung zum Frühjahrstreffen 1976 der Deutschen Malakozoologischen Gesellschaft in Schotten/Vogelsberg (Oberhessen) vom 27. bis 30. Mai. Schotten - im neu geschaffenen Vogelsbergkreis - liegt am Rande des Naturparkes "Hoher Vogelsberg." Die Stadt ist mit dem PKW zu erreichen: von Norden: Autobahn Kassel-Frankfurt = Abfahrt Giessen-Nord (Reiskirchen) - B 49 nach Grünberg - dort nach Laubach abbiegen - B 276 nach Schotten; hier: am Ortseingang liegt rechts eine Tankstelle, es folgt eine Linkskurve in die Stadt hinein, gleich dahinter biegt nach links die Einfahrt zum Hotel Haus Sonnenberg ab (auf der rechten Seite das Schwimmbad); von Süden: Autobahn Frankfurt-Kassel = Abfahrt Giessen-Mitte (Steinbach) - B 457 nach Lich - dort nach Laubach abbiegen - B 276 nach Schotten. Weiter wie oben; von Süd-Osten: Autobahn Würzburg-Frankfurt = Abfahrt Kleinostheim (hinter Aschaffenburg) - Hanau - Langenselbold - Liebs - dort auf die B 457 nach Bldingen - Nidda - B 455 nach Schotten; hier: durch den Ort in Richtung Laubach/Grünberg/Giessen bis zum Schwimmbad auf der linken Seite, rechts liegt die Auffahrt zum Hotel Haus Sonnenberg; von Süden und Westen: über die Autobahn (Frankfurter bzw. Gambacher Kreuz) zur Autobahn Frankfurt-Kassel, dort wie "von Süden."

Tagungsstätte: das Hotel "Haus Sonnenberg" in Schotten mit Tagungsräumen, eigenem Schwimmbad, etc., sowie Übernachtungsmöglichkeit für alle Teilnehmer. Anmeldung: a) an die unten genannte Anschrift; b) direkte Zimmerbestellung beim Hotel "Haus Sonnenberg." Für beide Anmeldungen liegen Formulare bei. Anmeldetermin: spätestens bis zum 15. März 1976.

Vorläufiges Programm. 27. Mai: Im Laufe des Tages Eintreffen der Teilnehmer. Abends: zwangloses Beisammensein im Hotel "Haus Sonnenberg." 28. Mai: Vormittags und nachmittags: Busfahrt durch den Vogelsberg; Erlenbruchwald in der montanen Region; Ulrichstein (Schlossberg mit *Clausilia parvula*-*Discus rotundatus*-Coenose); dort auch Mittagessen; Weiterfahrt zum Hochmoor, den Forellenteichen und dem Taufstein (*Phenacolinax major*, *Bythinella d. compressa*, u.a.); nach Wunsch Spaziergang vom Taufstein zum Hoherodskopf (eventuell zum Kaffeetrinken im Club-Haus des Vogelsberger Höhen-Clubs). Abends: Hotel "Haus Sonnenberg." 29. Mai: Vormittags und nachmittags: Busfahrt durch den südlichen Vogelsberg in das Steinebachtal (Trockenrasen-Coenosen); zuden Mooser Teichen; nach dem Mittagessen zum Hoherodskopf und Besichtigung der Forschungsstation "Künanz-Haus" (Ausstellung über die bisherige zoologische Forschungsarbeit). Abends: Mitgliederversammlung. 30. Mai: Eventuell kleinere Exkursionen in die Umgebung von Schotten; nach dem Mittagessen Abreise.

Anfrage, etc.: Dr. J. H. Jungbluth, Zoologisches Institut I, 69 Heidelberg, Im Neuenheimer Feld 230.

SIXTH EUROPEAN (= INTERNATIONAL) MALACOLOGICAL CONGRESS. — Preliminary Announcement. The Sixth European (= International) Malacological Congress will be held in Amsterdam, the Netherlands, in August, 1977, under the presidency of Dr. A. C. van Bruggen. The Congress will have its headquarters in the Free University and will be multidisciplinary in nature in order to appeal to as many malacologists as possible. Emphasis will be on neurophysiology, endocrinology, embryology, etc., as well as on the more traditional topics such as taxonomy, zoogeography and morphology. First circulars will be mailed in the 1st half of 1976; it is our intention that the mailing list will cover anybody working with molluscs anywhere in the world. Anyone not expecting to be on the mailing list (through malacological or conchological societies or organisations such as neurophysiological symposia, embryological seminars, etc.) should have their name registered with the Secretary General of the Congress, Dr. E. Gittenberger, Rijksmuseum van Natuurlijke Historie, Raamsteeg 2, Leiden, Netherlands.

AMERICAN MALACOLOGISTS, 1975 SUPPLEMENT. — The 1975 Supplement to the *American Malacologists* was published in June 1975 and consists of pages 495-600. It may be obtained for US \$2.00 from American Malacologists, P. O. Box 4208, Greenville, Delaware 19807, U.S.A.

The second edition of *American Malacologists* will probably appear in 1977.

A BIOBIBLIOGRAPHY OF WILLIAM HARPER PEASE, MALACOLOGIST OF POLYNESIA. — Workers in the field of Polynesian natural history now have a very useful and informative account of the life of William Harper Pease. In a joint paper recently published in *Nemouria* at the Delaware Museum of Natural History, Drs. E. Alison Kay and William J. Clench have outlined the life of this unique 19th century conchologist (1824-1871) who lived in Hawaii from 1849 until his death. He published 67 articles on natural history, most of which dealt with approximately 660 new species and genera of mollusks.

The carefully prepared catalogue of species, accompanied by original references and type localities, will save workers many hours of search and will contribute to a higher quality of research in the future by those who use this work. A sample of Pease's handwriting is given for those trying to identify old shell labels. A list of the old geographical names and their modern equivalents are given, as for example: Ascension Island is now Ponape, Caroline Islands, and Bolabola is now Borabora in the Society Islands. This publication of 50 pages is Number 16 of *Nemouria* (Occasional Papers of the Delaware Museum of Natural History) and was published on December 30, 1975. Copies may be obtained for US \$2.00 each by remitting to the Delaware Museum, P. O. Box 3937, Greenville, Delaware 19807, U.S.A. — R. T. ABBOTT

WESTERN SOCIETY OF MALACOLOGISTS. — The 9th annual meeting of the Western Society of Malacologists will be held from 23-27 June 1976 on the Asilomar State Conference Grounds, Pacific Grove, California. The program will feature contributed papers, symposia, displays, shell auction and field trips. Inquiries about the meeting should be made prior to 1 May 1976 and addressed to Mr. Clifton Martin, 324 Kennedy Lane, Oceanside, California 92054. Applications for membership in the WSM should be sent to Mr. Mert Goldsmith, 1622 N. 20th Street, Phoenix, Arizona 85006. Annual dues are US \$5.00 for regular members, US \$1.00 for each additional family member and US \$2.00 for students. Regular members and students receive the *Annual Report* of the Society. — JAMES NYBAKKEN

OBITUARY



(1958)



(1973)

GILBERT PERCY WHITLEY

9 June 1903 - 18 July 1975

The untimely death of Gilbert Whitley meant the loss of one of Australia's best-known zoologists. Mr. Whitley's scientific contributions have encompassed many animal groups, although he was primarily an ichthyologist. One of his major interests in recent years was the history of zoology, particularly of ichthyology and malacology, in the Australian region. He published several bibliographic papers on Australian malacologists, including Joyce Allan, George F. Angas, Tom Iredale, William Denison (with T. Iredale), H. L. Kesteven and Charles Laseron (with D. F. McMichael), and also illustrated some of Tom Iredale's works on molluscs. He attributed much of his interest in historical and bibliographic matters to the inspiration of Tom Iredale. Both Whitley and Iredale worked in the Australian Museum in adjoining rooms for most of their working lives and remained firm friends until Iredale's death in 1972.

A detailed account of Gilbert Whitley's life and work is being prepared for publication elsewhere.

W. F. PONDER

BOOK REVIEWS

PULMONATES. Volume 1, Functional Anatomy and Physiology. Vera Fretter & J. Peake, Editors. Academic Press, London. 1975. xxx, 417 p, illus. £ 13.20, US \$ 35.00.

This 1st volume of a 2-volume set concerned with pulmonate gastropods is a compilation of reviews in areas relating to the functioning of the systems of the pulmonate body and also the embryology of the group. As Dr. Fretter notes in the Preface to the volume, pulmonates make up a large percentage of the gastropods and dominate the molluscan fauna of non-marine environments. The pulmonates have been increasingly utilized recently for physiological studies, especially in the area of neurophysiology, and the publication of a volume concerned exclusively with this group is a manifestation of the increased interest in pulmonates.

Included in Volume 1 are chapters dealing with 8 topics: locomotion; respiration; alimentary canal; water relationships; nervous system, eye and statocyst; endocrinology; reproduction; and development.

Chapter 1, Locomotion, covers the general arrangement of muscle fibers, using *Helix* as a representative pulmonate; methods of muscular locomotion, with a description of types and mechanisms of muscular waves on the sole of Stylommato-phora; ciliary locomotion; posture, body movements and the hydrostatic skeleton. In all categories except arrangement of muscle fibers, the aspects of locomotion of various genera are compared.

Chapter 2, Respiration, covers the lung, respiratory exchange, respiratory pigments and oxygen consumption. The authors seem to have tried to eliminate discussion of facts which have been previously reviewed and, in doing so, have left the reader with little integrated information on respiration in pulmonates. Description of the pulmonary cavity and its modifications in the pulmonates is very general. A more informative and comparative view of the pulmonate respiratory apparatus is given in the Introduction. The brief summary of hemocyanin provides very little factual information. The discussion of oxygen consumption is somewhat more informative, but in many instances the coverage is too general. Some material presented in Chapter 4 should have also been included in this section. There is almost no functional anatomy of the pulmonary cavity or circulatory system included, which logically could have been provided. However, various aspects of the circulatory system are included in other chapters when they pertain to the topic under discussion.

Chapter 3, Alimentary canal, gives a good over-all picture of the functional anatomy of the entire digestive system from the mouth to the rectum and includes some recent works on the ultrastructure of the digestive gland, as well as generally describing the circulatory and nervous connections of each region. Physiologically, the chapter includes feeding, radula formation and digestive processes, with summaries of the digestive enzymes found in the various portions of the alimentary canal. Because the author concentrates on the digestive process, enzymes discussed and summarized are limited to those involved in digestion, and enzymes associated with other metabolic processes in the digestive gland are seldom mentioned.

Chapter 4, Water relationships, gives an excellent review of the physiological relationships of nearly every conceivable area, ranging from water content and osmotic concentrations, mechanisms and physiological consequences of water exchange to evolutionary considerations. Tables supplement the areas to facilitate comparisons of different genera. Included are topics which complement other chapters, e.g., metabolism and respiration, neurosecretion, water relationships of developing stages

and a brief description of the circulatory system. The chapter stresses physiological relationships and very little functional morphology is included.

Chapter 5, Nervous system, eye and statocyst, emphasizes the Stylommatophora and is mainly concerned with the central ganglia, with a brief description of the peripheral nerves in *Helix*. This coverage includes a comparison of a number of genera with regard to the morphology and physiology of the ganglia, transmitter substances, pharmacological studies, mapping and behaviour. The structure and physiology of the stylommatophoran eye is nicely described, as is the stylommatophoran statocyst, with little mention of the Basommatophora. The authors did a creditable job with a subject that probably deserves its own book.

Chapter 6, Endocrinology, is very complete and includes most of the work published on endocrinology of pulmonates. The chapter gives a comparative picture whenever possible. Subjects covered are morphology and function of endocrine structures, including the ganglia and associated structures, optic tentacle, gonad, and descriptions of neurosecretory cell types. The authors provide a good review of what is known of the function of endocrine structures in such areas as differentiation of sex cells, gametogenesis, ovulation and oviposition, growth and differentiation of the reproductive tract, osmotic equilibrium and ion transport and growth. Included are discussions of problems encountered in pulmonate endocrinology, e.g., the effects of tentacle extirpation on differentiation of sex cells in Stylommatophora.

Chapter 7, Reproduction, is nicely divided into sections which clearly demonstrate the organization, functional anatomy and physiology of the pulmonate reproductive system. The section regarding the organization of the genital system is a comparative section and includes families of the lower Basommatophora, Hygrophila, the Succineidae and higher Stylommatophora. The section dealing with the functional anatomy and physiology of the reproductive system covers the Basommatophora and Stylommatophora in about equal amounts as do the remaining sections concerned with egg capsules, reproductive cycles, copulation and oviposition. The chapter well integrates the functional anatomy and physiology of the reproductive system in pulmonates and is very helpful due to its comparative nature. Something which could have been mentioned is the presence of agglutinins in the stylommatophoran albumen gland, where they are particularly common.

Chapter 8, Development, covers the developmental process from oogenesis to organogenesis. Much of the chapter is from a previously published review article by the same author, but there are additions and the material has been constructed to be pertinent to pulmonates. Each section includes functional anatomy and physiology of development in Basommatophora and Stylommatophora.

I feel that this volume will be useful as a starting point for information on pulmonates without having to extract the pulmonate portions from the remainder of the Mollusca included in most other compilations. The subjects are reasonably well covered and up to date. A book such as this is necessarily behind the current work being published, especially in a rapidly expanding area such as neurophysiology. A reader who expects to learn all about the functional anatomy and/or physiology of pulmonates will realize that the coverage is far from complete. The circulatory system, although discussed in various chapters in a limited way, could be covered in its entirety in a complete section. The functional morphology of the kidney deserves inclusion somewhere, and there is almost no mention of the heart.

A reader who is interested in a particular area covered, especially if not very familiar with the area prior to reading this volume, will find Volume 1 helpful, and the volume should stimulate further interest in pulmonates.

PAUL H. RUDOLPH

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Ann Arbor, Michigan 48109, U.S.A.*

CONTENTS OF CURRENT SERIAL PUBLICATIONS ON MOLLUSKS

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der Senckenbergischen Naturforschenden Gesellschaft
Organ der Deutschen Malakozoologischen Gesellschaft

Begründet von Prof. Dr. W. KOBELT
Weitergeführt von Dr. W. WENZ und Dr. F. HAAS
Herausgegeben von Dr. A. ZILCH

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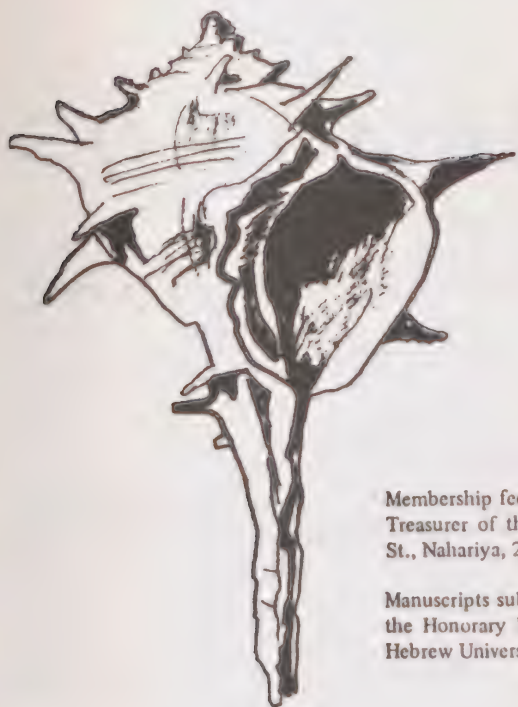
The non-marine aquatic Mollusca of Thailand.

By

ROLF A. M. BRANDT.

With 30 plates.

Frankfurt am Main 1974



ARGAMON ארגמון

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Rijksmuseum van Natuurlijke Historie
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COMUNICACIONES DE LA Sociedad Malacológica DEL Uruguay

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EDITED BY

R. TUCKER ABBOTT

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ALL RECEIPTS from the sale of INDO-PACIFIC MOLLUSCA are invested in the Journal itself or expended directly to promote malacological research. Inquiries concerning subscriptions should be addressed to INDO-PACIFIC MOLLUSCA, Department of Mollusks, Academy of Natural Sciences, Philadelphia 3, Pennsylvania, U.S.A. The Journal is not sent to libraries as an Academy publication exchange. Contributions of specimens of Indo-Pacific marine mollusks for the advancement of research may be mailed to the Curator, Department of Mollusks at the Academy or to specialists currently working on particular genera or families.

Instructions for Binding

THERE ARE no special instructions for binding, since the numbers are issued in consecutive pamphlet form of four or more pages. Each volume contains approximately 300 pages with an index at the end. Consecutive pagination, for bound copies, appears in the normal place at the top right or left of each page.

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The Natural Science Foundation

THE NATURAL SCIENCE FOUNDATION is a tax-exempt scientific and educational organization incorporated in 1953 in Pennsylvania for the purpose of encouraging and promoting research and education in the natural sciences, particularly in malacology. It sponsors and helps finance INDO-PACIFIC MOLLUSCA, and has supported numerous expeditions for mollusks in the Indian and Western Pacific Oceans. Copies of annual reports are available upon request. Inquiries concerning membership should be sent to the Natural Science Foundation, 1510 Chestnut Street, Philadelphia 2, Pennsylvania.

March 31, 1959

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Introduction 5

INTRODUCTION

INDO-PACIFIC MOLLUSCA is a journal devoted to the taxonomic revision of the marine mollusks of the tropical Western Pacific and Indian Oceans. For two hundred years many thousands of Indo-Pacific mollusks have been described in numerous and widely scattered publications with little or no correlation with previous reports nor in relation to species described from other nearby islands and provinces of this rather uniform region. This has resulted in many synonyms, the unwarranted treatment of some forms as full species, wide variation in nomenclature, and, in some cases, considerable duplication of research and effort.

Purpose of the Journal

Although taxonomic malacology, particularly of the Indo-Pacific, is to a great extent still in the descriptive and cataloging stages, with many new species yet to be described, it has seemed advisable to begin this series of taxonomic monographs, so that all the available information can be drawn together and a careful evaluation made of the known species. While the monographs in this journal may be considered to be "up to date", experience tells us that no scientific effort is either perfect or complete. Newly collected material, a re-examination of characters, differences of opinion, or necessary revisions in nomenclature all contribute towards changes, a better understanding and an improved classification of species.

Method of Publication

To help reduce the confusion caused by additions and changes which inevitably arise when a new monograph stimulates further research, this journal is published in a form which permits it to be either bound in the normal manner or kept in looseleaf fashion. While most of our efforts will be directed towards genera and families that are still in need of revision, there will be some effort to keep previously published monographs "up to date" by adding newly discovered species, important changes in nomenclature or new information concerning habitats, geographical records and anatomy. These supplements will be issued at the close of each volume in the form of a Review Number, and those subscribers maintaining their journal in looseleaf form need only slip the additional pages in the appropriate places. Monographs will be undertaken in groups where sufficient material and

competent specialists are available. Numbers will be published at irregular intervals, as research is completed, but it is hoped that a yearly minimum of a hundred pages will be maintained.

Regional Scope of the Journal

This journal attempts to cover the species which are mainly confined to the extensive tropical marine region known as the Indo-Pacific. This is a fairly uniform province embracing the Indian and tropical West Pacific Oceans. It extends from the east coast of Africa across the Indian Ocean (to the north half of Australia and the south half of Japan) and eastward through the Hawaiian Chain and Polynesia to Easter and Clipperton Islands. In malacological terms, the Indo-Pacific may be generalized as that region coinciding with the distribution of such common species as *Cypraea caput-serpentis* Linné, *Conus ebraeus* Linné, *Nerita albicilla* Linné and *Antigona reticulata* (Linné). Within this region there are several provinces which contain endemic species or exclude certain otherwise widely distributed species.

In cases where a genus or family is predominantly Indo-Pacific, the few additional species which occur in other regions of the world will also be included. Pelagic groups, such as *Janthina*, *Recluzia*, the Pteropods, and certain cephalopods will be treated from a worldwide standpoint because of their universal distribution.

Scientific Names

The scientific names employed by the authors of these monographs are those which are considered to be the most acceptable under the present rules and recommendations set down by the International Commission on Zoological Nomenclature. When personal opinion is involved, the name most widely used has been accepted.

Synonymies

The first reference under the species heading is to the original citation, and all subsequent references are to known or supposed synonyms. Other references may be included to demonstrate previous general placement or lead to additional information, such as anatomy, habits, new localities, etc. The geographical name appearing in parentheses refers to the original locality as cited by the author.

Measurements

Measurements of specimens are made in millimeters (25.37 mm. = 1 inch). Except where extensive measurements may be necessary, we generally list only an example of a *large* (the largest we have

March 31, 1959

INDO-PACIFIC MOLLUSCA, vol. 1, no. 1

Vasum 15

THE FAMILY VASIDAE IN THE INDO-PACIFIC

by R. TUCKER ABBOTT

Pilsbry Chair of Malacology
Academy of Natural Sciences of Philadelphia

November 23, 1960

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THE GENUS STROMBUS IN THE INDO-PACIFIC

by R. TUCKER ABBOTT

Pilsbry Chair of Malacology
Academy of Natural Sciences of Philadelphia

September 28, 1961

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by R. TUCKER ABBOTT

Pilsbry Chair of Malacology
Academy of Natural Sciences of Philadelphia

September 26, 1961

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THE FAMILY PINNIDAE IN THE INDO-PACIFIC

by JOSEPH ROSEWATER

Division of Mollusks
United States National Museum
Washington, D. C.

March 31, 1964

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THE FAMILY TURRIDAE IN THE INDO-PACIFIC

Part 1. The subfamily Turrinae

by A. W. B. POWELL

Auckland Institute and Museum
Auckland, New Zealand

April 30, 1965

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THE FAMILY TRIDACNIDAE IN THE INDO-PACIFIC

by JOSEPH ROSEWATER

Division of Mollusks
United States National Museum
Washington, D. C.

April 30, 1965

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by WILLIAM K. EMERSON

Chairman and Associate Curator
Department of Living Invertebrates
American Museum of Natural History

April 30, 1965

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by TAKASHI OKUTANI

Tokai Regional Fisheries Research
Laboratory, Tokyo, Japan

April 30, 1965

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MIOCENE STROMBUS (DOLOMENA) FROM INDIA

by R. TUCKER ABBOTT

Pilsbry Chair of Malacology
Academy of Natural Sciences of Philadelphia

May 15, 1967

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Turridae 409

THE FAMILY TURRIDAE IN THE INDO-PACIFIC

Part 1a. The subfamily Turrinae concluded

by A. W. B. POWELL

Auckland Institute and Museum
Auckland, New Zealand

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by PETER JUNG

Naturhistorisches Museum, Basel, Switzerland

and R. TUCKER ABBOTT

Pilsbry Chair of Malacology
Academy of Natural Sciences of Philadelphia

May 15, 1967

INDO-PACIFIC MOLLUSCA, vol. 1, no. 7

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STROMBUS (CANARIUM) WILSONI NEW SPECIES
FROM THE INDO-PACIFIC

by R. TUCKER ABBOTT

Pilsbry Chair of Malacology
Academy of Natural Sciences of Philadelphia

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by BARRY R. WILSON

Western Australian Museum, Perth

and JENNIFER A. MCCOMB

University of Western Australia, Perth

INDO-PACIFIC MOLLUSCA

VOLUME 2

EDITED BY

R. TUCKER ABBOTT

*Monographs of the Marine Mollusks of
the World with Emphasis on those of the
Tropical Western Pacific and Indian Oceans*

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August 30, 1968

INDO-PACIFIC MOLLUSCA is a professional journal devoted to the systematics and taxonomy of the marine mollusks, both living and fossil, of the world, but with emphasis on those of the tropical Western Pacific and Indian Oceans.

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The journal was originally sponsored and financed by the Natural Science Foundation, a tax-exempt organization that existed between 1953 and 1964. The journal is now self-supporting and continues to be published at the Academy of Natural Sciences of Philadelphia.

August 30, 1968

INDO-PACIFIC MOLLUSCA, vol. 2, no. 9

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TWO BINDERS

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° Text in preparation

August 30, 1968

INDO-PACIFIC MOLLUSCA, vol. 2, no. 9

Cassidae 15

THE HELMET SHELLS OF THE WORLD (CASSIDAE). PART 1.

by R. TUCKER ABBOTT

Pilsbry Chair of Malacology
Academy of Natural Sciences of Philadelphia

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Editor: R. Tucker Abbott
du Pont Chair of Malacology
DELAWARE MUSEUM OF NATURAL HISTORY
Greenville, Delaware 19807, U.S.A.

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by A. W. B. POWELL
Auckland Institute and Museum
Auckland, New Zealand

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by JOSEPH ROSEWATER
Division of Mollusks
National Museum of Natural History
Washington, D.C. 20560 U.S.A.

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Part II. The Subfamilies Tectariinae and Echininae

by JOSEPH ROSEWATER
Division of Mollusks
National Museum of Natural History
Washington, D.C. 20560 U.S.A.

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INDO-PACIFIC MOLLUSCA

*Monographs of the Marine Mollusks of the World with Emphasis
on those of the Tropical Western Pacific and Indian Oceans*

EDITED BY

R. TUCKER ABBOTT

VOLUME 3

Published by

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Box 3937, Greenville,
Delaware 19807, U.S.A.

THE GENUS DRUPA IN THE INDO-PACIFIC

by WILLIAM K. EMERSON
Department of Living Invertebrates
The American Museum of Natural History
New York, N.Y. 10024
and
WALTER O. CERNOHORSKY
Auckland Institute and Museum
Auckland, New Zealand

volume 3, no. 14

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- 2. Title page to Volume 3. (put in Binder 1).
- 3. List of Issues published as of June 1, 1973. (put in Binder 1).
- 4. Replacement Pages for *Tectarius* (8 pages of corrections for "The Family Littorinidae in the Indo-Pacific. Part II." Put these 4 sheets in their proper place in Binder 1 by following the looseleaf page numbers at the bottom of the page (i.e. [05-443]). Remove and place the obsolete pages at the end of Binder 3, just after the guide tab "Replaced Pages."

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THE GENUS *GABRIELONA* (PHASIANELLIDAE) IN THE INDO-PACIFIC AND WEST INDIES

by ROBERT ROBERTSON

Pilsbry Chair of Malacology
The Academy of Natural Sciences of Philadelphia

November 27, 1973

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by A. W. B. POWELL

Auckland Institute and Museum
Auckland, New Zealand

November 27, 1973

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THE FAMILY HARPIDAE OF THE WORLD

by HARALD A. REIDER

Division of Mollusks
National Museum of Natural History
Smithsonian Institution
Washington, D. C.

The Journal of Conchology

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PUBLISHED BY THE CONCHOLOGICAL SOCIETY
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della
Società Malacologica Italiana

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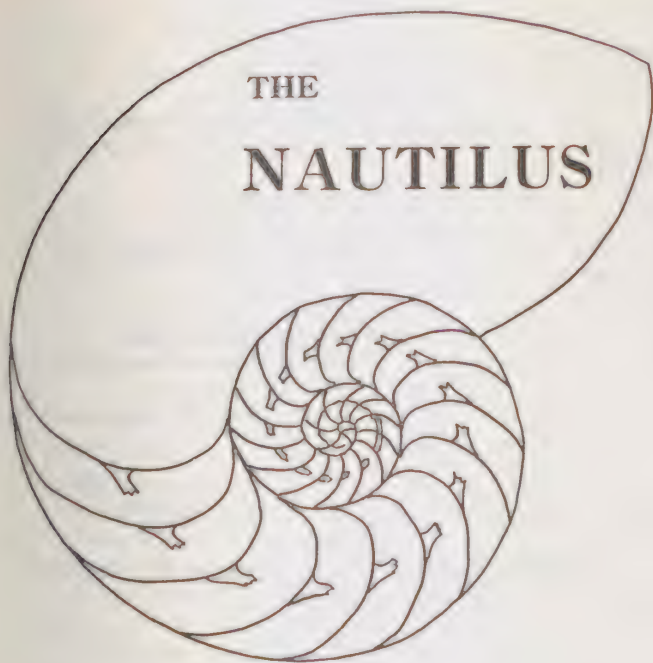
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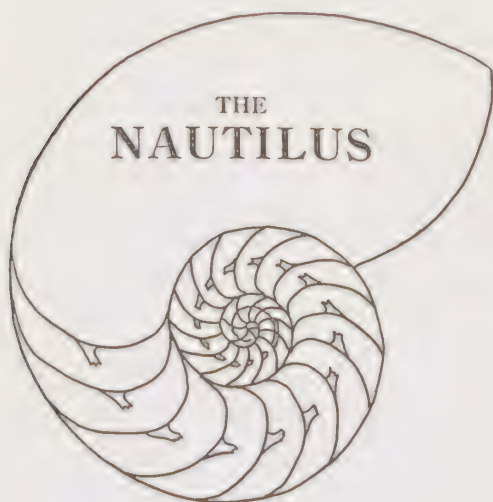
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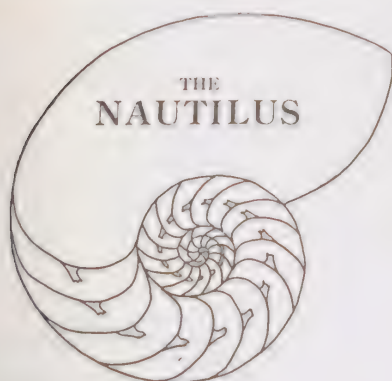
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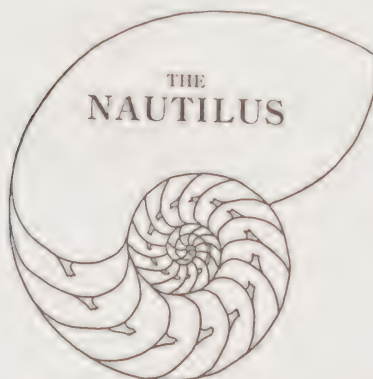
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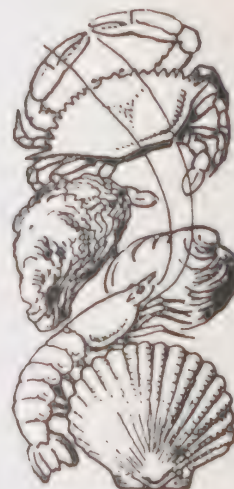
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ORDER, Suborder, DIVISION, Subdivision, SECTION,
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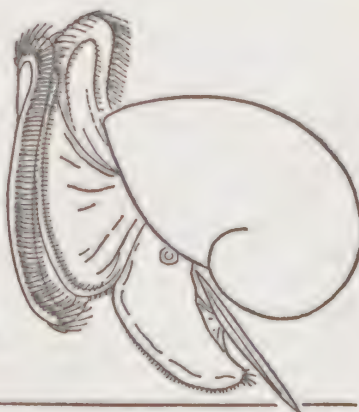
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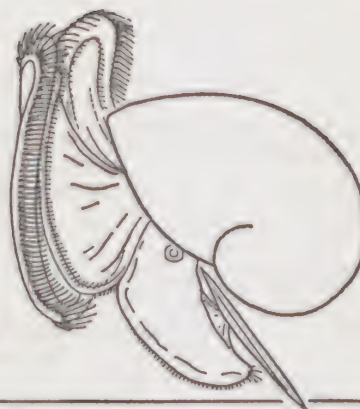
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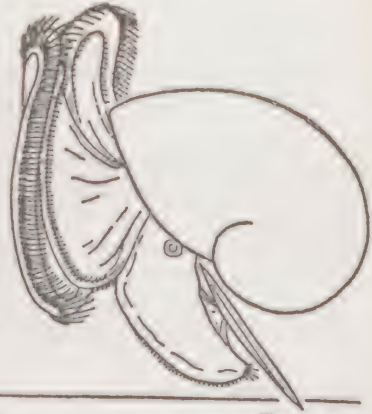
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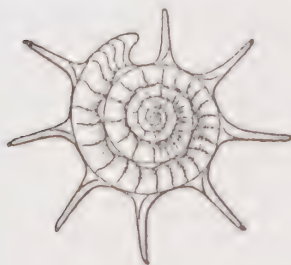
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